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THE TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

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Clerk of Publications . . . G. B. STRATTON, M.B.E.

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OBSERVATIONS ON THE TOXOGLOSSAN GASTROPOD *MANGELIA BRACHYSTOMA* (PHILIPPI)

BY

ELIZABETH ROBINSON (REA), M.Sc.

Department of Zoology, Birkbeck College, University of London

[Accepted 9th February 1960]

(With 4 figures in the text)

The proboscis of *Mangelia* is a highly specialized and modified organ involving a terminal sucker and an additional permanent sheath within the proboscis sac which has been named the supporting sheath. Its structure can be derived from the condition seen in the Conidae by supposing that the folds formed during the retraction of the proboscis in these animals become lengthened to form one single permanent fold in *Mangelia*. The anterior part of the alimentary canal and the organs associated with it are similar to those found in the Conidae, and include a highly coiled poison gland which opens ventrally into the oesophagus immediately posterior to the opening of the buccal sac. It is pointed out that the poison gland is the coiled tube and that the swollen proximal end of the gland is a non-glandular propulsive organ, the muscular bulb, and that the true poison gland duct is a short distal passage joining the tubular gland to the buccal cavity. The frequently stated belief that the poison gland is derived from the gland of Leiblein is discussed and the possibility that it represents the ventral salivary glands is mentioned. The absence of a pedal sucker and of the ventral pedal gland is noted. The genital ducts are described and found to conform to the general plan seen in the Stenoglossa.

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INTRODUCTION

The toxoglossan prosobranch molluscs have long been known as predators overpowering their prey by means of a toxic secretion, the most feared being the members of the family Conidae, particularly frequent on the coasts of the Pacific Ocean, whose bite (see Yasiro, 1939) is occasionally fatal to man. No conids occur in British waters, though members of another toxoglossan family, the Pleurotomatidae, may sometimes be found, with feeding habits that seem to be similar to those of the better known cones. They are never abundant, but occur moderately often in sandy or muddy sand bottoms at low water of spring tides or below. The animal which is described is one of the more easily obtained British pleurotomids, indentified as *Mangelia brachystoma* (Philippi) by the British Museum (Natural History). It is dredged on muddy sand at a depth of 4–8 m. in Plymouth Sound, and seems to belong to the infauna, pushing

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through the sand in search of prey. What this may be is unknown, as the animals refuse to feed in captivity and nothing recognizable can be obtained from their gut ; the other common animals of the habitat are tanaid crustaceans and the polychaete worms *Melinna palmata* and *Lumbriconereis latreilli*. Since other toxoglossans appear to feed primarily on annelids or molluscs or fish (Kohn, 1959) it may be that *Mangelia brachystoma* also subsists on the worms available in the habitat in which it lives.

The animals were examined for the most part alive and were dissected after being anaesthetized in 7 per cent magnesium chloride solution, using a high-power binocular microscope. For histological investigation animals were fixed in one of Bouin's Helly's or Ciaccio's fluids and usually stained in Heidenhain's iron haematoxylin.

GENERAL MORPHOLOGY

Mangelia brachystoma has a slender cone-shaped shell which is coiled in a dextral spiral and may be as much as 11 mm. long with a width equal to about one-third of this. The outer lip of the shell is produced to form a short siphonal groove which accommodates the inhalant siphon (Fig. 1, IS) of the mantle in the living animal, but except for this it is simple. There is no operculum. The animal can retract completely into the shell, when the only visible parts are the base of the foot and the siphon lying within the shell on the left side of the animal. On the right side the exhalant aperture (ES) leads from the mantle cavity bounded on either side by a ridge of ciliated epithelium. The mantle edge is thickened to form a slight collar (C) produced into two small lappets at the base of the inhalant siphon : these direct the flow of water into the mantle cavity.

When the animal is extended the head and foot are seen to be separated from the visceral hump by a moderately long neck (NK). These structures are translucent in the living animal with white blotches at frequent intervals under the surface. The head (H) bears a pair of tentacles (T) anteriorly, which can be retracted until they are little more than small knobs. On their outer surface they bear a black eye (E). The head projects between the tentacles as a short snout, bearing the apparent mouth on its anteroventral surface. This is a dorso-ventral slit, with crenated edges when closed, which can expand to form a wide opening into a large introvert, within which lies the true mouth.

The foot (F), when extended, has an elongated triangular sole, the base of the triangle directed anteriorly, the apex posteriorly. Along the straight anterior edge runs a lappet, below which lies the pedal groove (PGR), the opening of the anterior mucous gland. In addition occasional mucous cells are seen on the upper surface and numerous cells secreting a mucoid substance are found on the sole. There is neither ventral pedal gland nor pedal sucker in either sex.

The mantle cavity is wide and slightly depressed. Water is directed into it by way of the inhalant siphon and leaves by the exhalant siphon, and away from these two openings the cavity is effectively separated from the exterior by the collar. The leaflets of three organs are suspended into the cavity from the mantle skirt. The bipectinate osphradium (O) is found anteriorly on the extreme left where water from the base of the siphon impinges against it ;

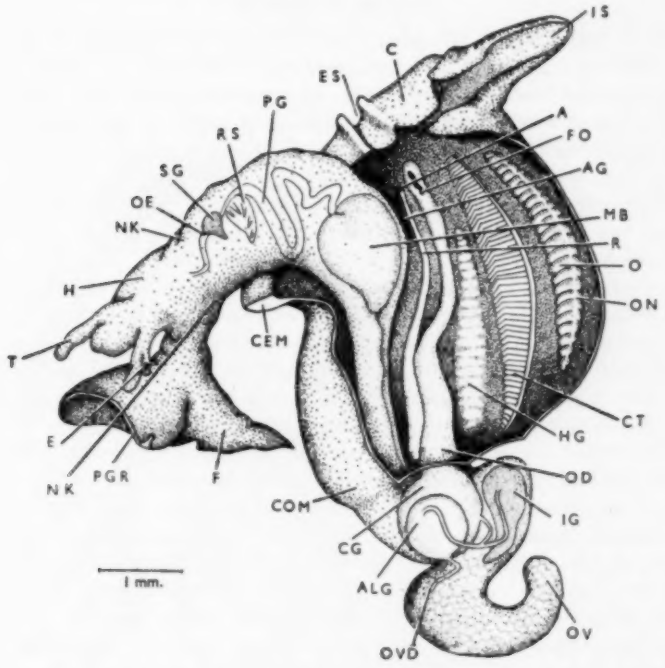

Fig. 1.—Female removed from shell and mantle cavity opened on left side to reveal its contents. Some organs in the body are seen by transparency.

A, anus ; AG, anal gland ; ALG, albumen gland ; C, collar ; CEM, cut edge of mantle skirt ; CG, capsule gland ; COM, columellar muscle ; CT, ctenidium ; E, eye ; ES, exhalant siphon ; F, foot ; FO, female opening ; H, head ; HG, hypobranchial gland ; IG, ingesting gland ; IS, inhalant siphon ; MB, muscular bulb ; NK, neck ; O, osphradium ; OD, oviduct ; OE, œsophagus ; ON, osphradial nerve ; OV, ovary ; OVD, ovarian duct ; PG, poison gland ; PGR, pedal groove ; R, rectum ; RS, radular sac ; SG, salivary gland ; T, tentacle.

its leaflets are purplish with brown, crenated edges, one row separated from the next by a cream-coloured axis through which runs the osphradial nerve (ON). To the right of the osphradium is the extensive monopectinate ctenidium (CT) with pale orange-brown leaflets, and to the right of this the whitish tissue of the hypobranchial gland (HG). The rectum runs on the right side of the mantle cavity to open at the anus (A) near the exhalant aperture. Overlying the anterior part of the rectum (R) and extending as far as the anus is a greenish-black organ, the anal gland (AG). The sexes are separate in *Mangelia* and in the female the genital duct (OD) runs alongside the rectum on its left, opening anterior to the anus. In the male there is a long penis (Fig. 4, P) on the right side of the head ; at rest it is folded back, stretching almost to the posterior end of the mantle cavity. It is a translucent organ in which the central duct (PD) can be seen in living specimens. The vas deferens (RVD, PVD) is a narrow, white, coiled tube leading to the base of the penis.

DIGESTIVE SYSTEM

The aperture (Fig. 2, OI) which lies between the tentacles is not the true mouth, but the opening of an introvert which is everted through this aperture when the animal feeds, to give rise to an elongated proboscis. The proboscis even when protruded forms not a simple tube but a double structure of one tube lying within the lumen of another. The inner of these, the buccal tube (BT), has the mouth (M) at its anterior tip. The surrounding tube, formed entirely of introvert, acts as a supporting sheath (SS) for the buccal tube. The proboscis can be completely withdrawn into the proboscis sac (PS) formed by part of the introvert.

The proboscis sac occupies a space equal to the length of the neck, in which it is contained, and is about one-third as wide as long. In the living animal it appears orange-pink. Although the animal has not been observed feeding, the anatomy and histology of the proboscis suggest that it can be extended beyond the animal for a distance several times the length of the proboscis sac. The buccal cavity (BC) is longer than in a less specialized feeder and forms a tube surrounded by a very thick coat of muscle. The buccal tube can be projected through the opening of the introvert and extended beyond this for a long way, the lumen of the buccal cavity then becoming very narrow.

As already mentioned, the buccal tube is enclosed in a secondary, but separate, sheath of muscle and epithelium, formed by the outfolding of the wall of the proboscis sac near the base of the introvert where the former joins the wall of the buccal tube itself. This is the supporting sheath, which always encloses and supports the buccal tube, only the extreme anterior end of which has ever been observed to project beyond it. It is not a fold which is formed during retraction and straightened out again on eversion to give the proboscis greater powers of extension, for its position in relation to the buccal tube is relatively constant whether this organ be completely retracted or partially everted. Further, its inner and outer walls are so linked by connective tissue as to suggest that they bear a fairly constant relationship to one another. Complication arises from the fact that at its anterior end the supporting sheath is doubled so as to give two tubes one within the other, the inner of the two prolonged slightly beyond the outer and giving the whole structure a tapered appearance. The inner and outer walls of these two tubes are also connected by fibrous bands suggesting that they, too, are permanent structures and not formed by extra folding during retraction.

The supporting sheath is extremely muscular. It is never retracted as much as the buccal tube, which is generally found lying well within its lumen when fully retracted. However, during partial eversion, when both organs are still enclosed in the proboscis sac, and when everted, the tip of the buccal tube projects beyond the openings of the supporting sheath as a swollen disc (OS).

When the proboscis is fully retracted the proboscis sac can be divided into two distinct regions. The retracted proboscis apparatus occupies the posterior part of the proboscis sac : the anterior part forms an empty tube which is histologically different from the posterior part. The walls of this anterior region are thickly ciliated, the cilia being very long and arising from columnar

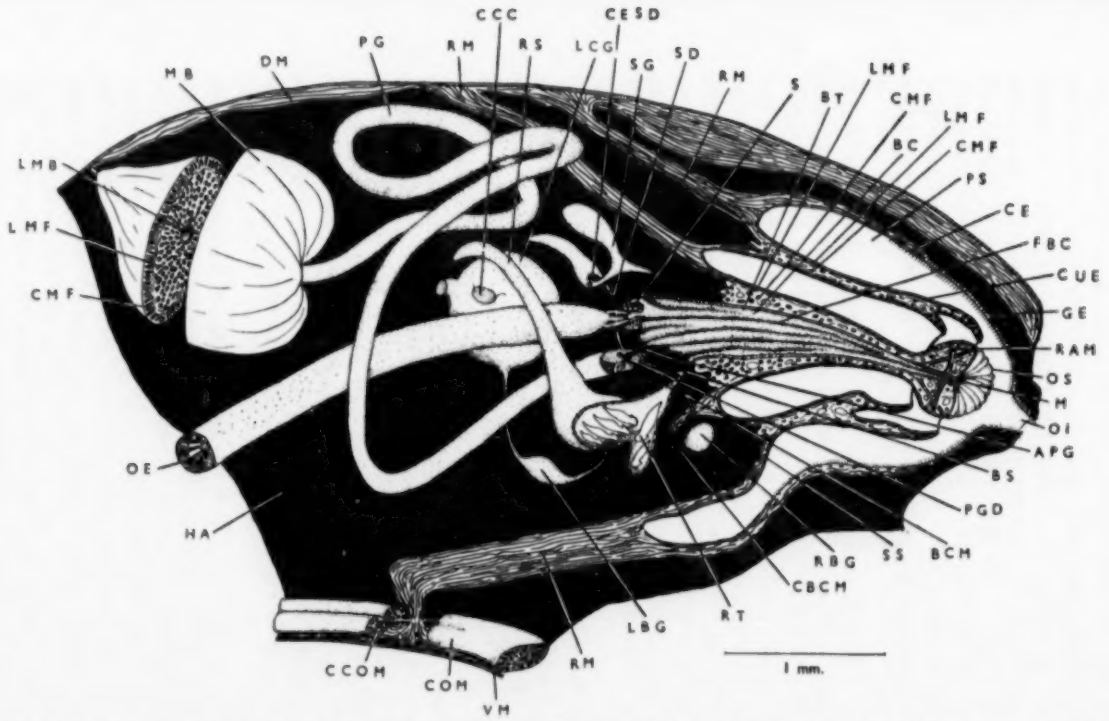

Fig. 2.—Lateral dissection of anterior part of body to show the proboscis, oesophagus and related organs, somewhat diagrammatic. The haemocoel is black. The buccal cavity, radular sac and poison gland have been opened.

APG, opening from poison gland to buccal cavity ; BC, buccal cavity ; BCM, buccal commissure ; BS, buccal sac ; BT, buccal tube ; CBCM, cut end of buccal commissure ; CCC, cut end of cerebral commissure ; CCOM, columellar muscle cut to show attachment of retractor muscles to ventral musculature ; CE, ciliated epithelium ; CESD, cut end of salivary duct ; CMF, circular muscle fibre ; COM, columellar muscle ; CUE, cuticularized epithelium ; DM, muscle of dorsal body wall ; FBC, folded wall of buccal cavity ; GE, glandular epithelium ; HA, haemocoel ; LBG, left buccal ganglion ; LCG, left cerebral ganglion ; LMB, lumen of muscular bulb ; LMF, longitudinal muscle fibre ; M, mouth ; MB, muscular bulb ; OE, oesophagus ; OI, opening of introvert ; OS, oral sucker ; PG, poison gland ; PGD, poison duct ; PS, proboscis sac ; RAM, radial muscle of oral sucker ; RBG, right buccal ganglion ; RM, retractor muscles of proboscis ; RS, radular sac ; RT, radular tooth ; S, sphincter ; SD, salivary duct ; SG, salivary gland ; SS, supporting sheath ; VM, muscle of ventral body wall.

epithelial cells wedged between large globular cells (GE) which appear to secrete drops of a clear liquid. This epithelial layer is linked to the connective tissues of the foot by strands of connective tissue and sparse muscle fibres. Although by comparison with the rest of the organ this part is served by a meagre musculature, it appears to be sufficient to prevent it from being everted with the rest of the proboscis. Posteriorly, in the region of the anterior part of the sheath and at the level of the mouth, the cilia are shorter and more sparse and the epithelial cells are cubical (CE). There are no secretory cells. The posterior part of the proboscis sac, which encloses the fully retracted proboscis, occupies approximately two-thirds of the whole sac. The epithelium which lines it is cuticularized (CUE) and longitudinal muscles fibre run below it forming a continuous sheath round the sac.

The supporting sheath is protected by a cuticularized epithelium (CUE) on both inner and outer surfaces. Immediately below these there are continuous layers of circular muscle (CMF) with layers of longitudinal muscle fibres (LMF) under them. The longitudinal muscles below the outer wall are numerous and are continuous with those of the wall of the proboscis sac, but those of the inner wall form a comparatively thin layer. The two layers are separated from one another by thick connective tissue with numerous blood spaces. The supporting sheath is thus seen to be a folding of the proboscis wall with two sheaths of circular muscle fibres inserted between the epithelium and the layer of longitudinal muscle fibres. It is exceedingly well innervated from the cerebral ganglia. Longitudinal muscle fibres continuous with those in the outer wall of the supporting sheath leave the base of the proboscis sheath as two large muscular bundles (RM), extending back into the body : one runs dorsally to join the muscles of the dorsal body wall and a mid-ventral tract passes back in the haemocoel, penetrates the columellar muscle (COM) and is inserted into the ventral body wall. The tip of the supporting sheath is narrow and cuticularized and the layers of epithelium, circular, and longitudinal muscle fibres are disposed exactly as they would be if the doubling of the distal end of the tube had been formed by an infolding of the wall. However, the permanence of this structure is demonstrated by the presence of radial fibres which bind the inner and outer walls of each concentric structure to one another. In the retracted state the walls of the supporting sheath are thrown into numerous fine transverse folds.

The buccal tube is also protected by an outer cuticularized epithelium without gland cells. A thin continuous layer of longitudinal muscle fibres (LMF) is found immediately below the epithelium which join with those from the supporting sheath to form the mid-ventral tract inserted in the ventral body wall. They are the retractor muscles of the proboscis. Internal to the layer of longitudinal muscle is an exceedingly thick sheath of circular muscle (CMF) which invests the buccal cavity from the mouth to the oesophagus. When the buccal tube is contracted this muscle causes the walls of the buccal cavity to be thrown into numerous longitudinal folds (FBC) so that the lumen is almost obscured.

When the buccal tube (Fig. 2, BT) protrudes from the supporting sheath (SS), its anterior tip enlarges to form a swollen disc (OS), directed slightly

downwards. The inner fold of the supporting sheath clasps the buccal tube around the base of this disc, while the outer fold stretches forward to clasp the margins of the disc. The mouth (M) opens centrally on the anterior face of the disc, at the focal point of numerous radial ridges formed by the puckering of the surface. These ridges may perhaps disappear during feeding, which has not been observed. When the proboscis is being moved freely outside the animal, transverse waves pass across the lower lip of the disc. The disc is made up of connective tissue, muscles and blood spaces, which when distended cause the otherwise tapered tip of the buccal tube to swell. A powerful ring of radial muscles (RAM) stretches from the inner to the outer wall of the disc. Contraction of these muscles reduces the size of the disc to the same dimensions as those of the buccal tube behind it, and allows the whole organ to retreat into the supporting sheath. Their contraction may also widen the cavity of the buccal tube and form a pumping mechanism for drawing up liquid food. Other muscle fibres run from the wall of the buccal cavity to the external surface of the disc in a radial direction. The antero-ventral surface of the disc is supplied with large mucous cells and is ciliated. The lateral and dorsal surfaces are covered by a cuticularized epithelium with numerous mucous glands.

The length of the gut from mouth to anus is short. Food passing in through the mouth enters the buccal cavity (BC) which, when the proboscis is everted to its fullest extent, must be a very long tube with an extremely narrow lumen, stretching from the mouth to a level just anterior to the nerve ring, where the buccal tube is separated from the oesophagus (OE) by a sphincter (S). When the proboscis is retracted the sphincter is found at the same level as the posterior limit of the proboscis sac. In preserved specimens the buccal tube is contracted and its wall folded into numerous longitudinal ridges (FBC).

The odontophore comprises the radula in the radular sac (RS) which is linked to the buccal cavity by a short tube, the buccal sac (BS) or bulb (Amaudrut, 1898). There are no odontophoral cartilages in *Mangelia*. The buccal sac opens on a ciliated papilla, slightly to the right of the mid-ventral line of the buccal cavity. It extends back along the right side of the buccal tube and widens to form the radular sac containing fully formed radular teeth (RT). The radular sac spreads posterodorsally over the oesophagus and its distal end is attached by fibres to the body wall on the left side. Muscle fibres can be seen in the wall of the radular sac, especially anteriorly, and these join the retractor fibres from the proboscis, and are inserted with them in the dorsal body wall. The radular teeth are long leaf-shaped plates borne in pairs ; they are thin, with the lateral edges curved to form a shallow trough. Distally the teeth taper to a sharp point, whereas basally they are thickened to form a solid insertion into the wall of the radular sac. Near the point of insertion on the outer side of each tooth is a sharp forwardly-directed cusp. The teeth are directed backwards when lying at rest in the radular sac. If the anterior part of the radular sac is folded upon itself due to retraction, the first few pairs of teeth sometimes appear to be directed anteriorly, but when the sac is pulled out, all the teeth will be found to be pointing backwards.

There is only one pair of salivary glands (Fig. 3, LSG, RSG). Both lie left of the oesophagus (OE) above the radular sac (RS) ; the duct (RSD) from

the right gland follows the course of the radular sac over the oesophagus to the right side where it discharges into the buccal sac (BS) ; that from the left gland (LSD) passes below the oesophagus to discharge into the buccal sac on the left. The openings from these two ducts into the buccal sac are symmetrical and mark the junction of the radular sac with the buccal sac. They are guarded by sphincters. The salivary tissue has only two kinds of cell, gland cells and supporting cells.

The epithelium lining the buccal sac is simple with no cilia or gland cells, and below this layer is a thin coat of longitudinal muscle fibres. When the proboscis is retracted the buccal sac is contracted to form a narrow tube joining the radular sac to the buccal tube. This region must be considered as part of the buccal tube, rather than part of the radular sac, since the salivary ducts discharge into it. Behind the opening of the buccal sac the character of the wall of the buccal cavity changes ; the folds of epithelium become less deep and dorsally they eventually disappear ; the cilia become shorter and sparser and the layer of underlying circular muscle becomes very thin ; ventrally the epithelial cells enlarge and are grouped longitudinally to form several thick pads which replace the simple epithelial ridges found more anteriorly ; the cilia on these pads are long and very thick and the underlying circular muscle of this region is not reduced to the same extent as it is dorsally. The ventral longitudinal pads gradually extend laterally and at the posterior end of the buccal cavity almost occlude the dorsal wall between them. A mid-ventral channel which is not ciliated is formed and this runs into the oesophagus. Large scattered gland cells are present in the epithelium of this region of the buccal cavity and become very numerous at the most posterior end.

Behind the opening of the buccal sac into the buccal cavity there is another opening also situated slightly to the right of the mid-ventral line. This is the opening of the poison duct (Fig. 2, PGD) which runs into one of the troughs between two ventral pads. The poison duct is very short and joins the poison gland (PG), a long tubular organ which passes back ventral to the radular sac. In living animals it has a white granular appearance. When the proboscis is retracted, the poison gland is folded back on itself in the dorsal region of the haemocoel. Its lumen is continuous at one end with its duct and at the other passes into a large pear-shaped muscular bulb (MB). This fills much of the body cavity, is exceedingly powerful, and is attached to the dorsal body wall at its blind end by a short strand of fibrous tissue. The lumen (LMB) is comparatively small and is lined by a single layer of cubical epithelial cells. The bulb is made of two muscular coats separated by a thin partition of connective tissue ; the inner one is four to eight times the thickness of the outer coat, and is made up entirely of longitudinal muscle fibres (LMF) which appear to be arranged in radial rows but may interlace slightly; the outer muscular coat is made up of circular, diagonal and a few longitudinal muscle fibres interdigitating with one another. The lumen of the poison gland is approximately circular in transverse section and is practically occluded by cilia arising from small supporting cells which cannot be seen clearly, although their elongated nuclei are sometimes distinguishable. There are only two kinds of cell in the poison gland, the supporting and the secreting cell, and these are arranged in a single layer

around the lumen. The gland cells are very large ; they are swollen at the base and taper distally. The cytoplasm contains granules of regular size, and only occasional cells are seen which are not completely filled with these. The lumen of the gland may contain secretion from these cells. The gland cells are supported on a basement membrane outside which is a coat of circular muscle fibres. The short duct of the gland, like that of the salivary gland, is a tube made of a single layer of cells surrounded by a muscular coat.

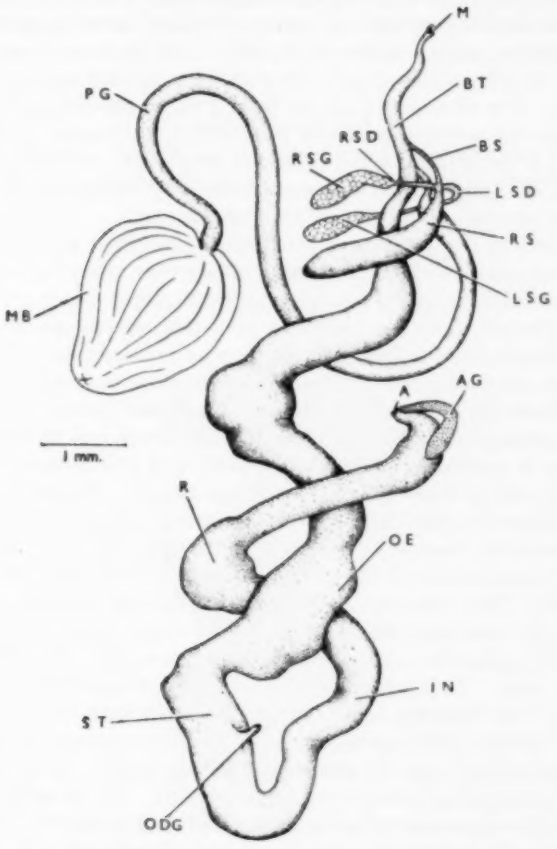

Fig. 3.—Diagram of the alimentary canal in dorsal view.
A, anus ; AG, anal gland ; BS, buccal sac ; BT, buccal tube ; IN, intestine ; LSD, left salivary duct ; LSG, left salivary gland ; M, mouth ; MB, muscular bulb ; ODG, opening from stomach to digestive gland ; OE, oesophagus ; PG, poison gland ; R, rectum ; RS, radular sac ; RSD, right salivary duct ; RSG, right salivary gland ; ST, stomach.

In fixed material the entry of the buccal cavity into the oesophagus is seen to be surrounded by a circular fold of epithelium which projects anteriorly into the lumen. This fold bears long cilia and circular muscle fibres run in it,

forming a strong sphincter (S). Behind this the narrow oesophageal tube passes through the nerve ring (LCG) and gradually widens as it passes posteriorly.

The wall of the oesophagus is folded longitudinally; it is lined by cuticularized columnar cells. Gland cells containing irregular-sized granules, similar to those seen in the posterior part of the buccal cavity, are present. Another type of gland cell with a granular cytoplasm also occurs and is especially numerous more posteriorly. This epithelial lining is surrounded by a coat of circular muscle fibres. The oesophagus extends along the left side of the body immediately below the body wall and comprises about half the total length of the gut.

The oesophagus crosses to the right side of the body and opens into the stomach (Fig. 3, ST), a change recognizable by a sudden absence of all kind of gland cells. The stomach in *Mangelia* is a short straight tube into which the oesophagus opens at one end and from which the intestine (IN) opens at the other. It is surrounded by a muscular coat. The walls of the stomach are not folded, but longitudinal ridges are formed by certain tracts of epithelial cells which are elongated and project into the lumen.

The structure of the stomach is most easily described by dividing it arbitrarily into three regions which grade into one another ; they are an anterior region, the region of the opening into the digestive gland (ODG) and a posterior region. The first of these is continuous with the oesophagus, its walls being thrown into longitudinal ridges, but no regular arrangement of these can be detected. The epithelial cells forming the ridges are covered by a very thin cuticle penetrated by dense cilia. No gland cells are present. Just anterior to the single opening of the digestive gland, the stomach wall becomes flattened, the epithelium is regular in shape and ciliated, and this flattened area is bordered on either side by a patch of elongated gland cells. Posterior to the opening into the digestive gland the region of flattened epithelium becomes very narrow and forms the base of a deep channel, the side walls of which are formed by a posterior continuation of the two glandular strips interspersed with ciliated epithelial cells. This channel leads directly from the posterior part of the stomach into the intestine, where the glandular region ends.

The digestive gland is very large and, with the gonad, fills all the posterior whorls of the body. It is a racemose gland in which one type of cell predominates. This is the digestive cell, always distended with very large numbers of spherules, though their appearance and staining properties vary greatly. One other kind of cell may be seen although only present occasionally. This is triangular in shape and has a very large nucleus. In material treated with acid fixatives the cytoplasm appears vacuolated as if numerous spherules have been dissolved. It is probable that these are calcium cells.

The intestine is a long straight tube which narrows as it passes anteriorly. There are no gland cells—in fact the lumen of the intestine is lined by only one kind of cell, cubical and bearing dense cilia. The rectum opens into the mantle cavity through the anus (A) on a small papilla. In the region round the anus mucus-secreting cells are found. The anal papilla is found a short distance behind the exhalant siphon (Fig. 1, ES).

Overlying the terminal part of the rectum and opening directly into it at the level of the anus is a small gland. In living specimens it can be seen as a

short dark streak below the body wall when the mantle cavity is opened, its diameter approximately the same as that of the rectum. This is the anal gland (Fig. 3, AG), a simple blind diverticulum lying in a small haemocoel. In the region of the anus, numerous amoebocytes are often aggregated and may be associated with the functioning of the gland. Only one kind of cell is seen in this gland and there are no cilia. The cells are fairly elongated and are borne on a basement membrane ; they are filled with greenish-brown granules which are especially dense near the free surface of the cell. Similar granules are also seen in the lumen of the gland lying close to the secretory cells. In certain Stenoglossa this gland has been shown to have an excretory function (Fretter, 1946).

GENITAL SYSTEM

The testis (Fig. 4, TS) overlies the digestive gland mainly on the columellar side of the posterior whorls of the body. It opens into the gonadial duct (GD)

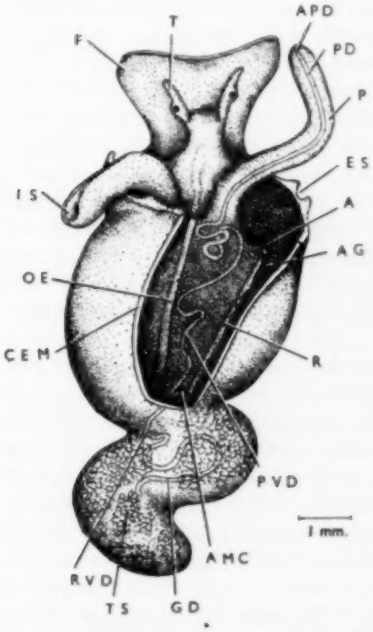

Fig. 4.—Male removed from shell and mantle cavity opened to show genital duct. A, anus ; AG, anal gland ; AMC, opening of vas deferens to mantle cavity ; APD, opening of penial duct ; CEM, cut edge of mantle skirt ; ES, exhalant siphon ; F, foot ; GD, gonadial duct ; IS, inhalant siphon ; OE, oesophagus ; P, penis ; PD, penial duct ; PVD, pallial vas deferens ; R, rectum ; RVD, renal vas deferens ; T, tentacle ; TS, testis.

which passes forwards to join the vas deferens (RVD, PVD). The gonadial duct is a fairly wide coiled tube which in adult specimens contains sperm ; it is lined by cubical epithelium with large spherical nuclei, and is surrounded by a thin layer of circular muscle ; it opens into the next section of the genital

duct, the renal vas deferens (RVD), through a sphincter. The vas deferens is divided into renal and pallial portions, the renal part is short and lies near the heart, the pallial part (PVD) is long, running below the body wall, near its junction with the mantle skirt, to the base of the penis (P). The renal vas deferens is a uniform straight tube lined by cubical epithelium with large spherical nuclei, heavily ciliated and with no gland cells ; at each end the duct is guarded by a sphincter and along its length it is surrounded by a thin musuclar coat. In one fixed specimen examined, sperm were seen in the extreme posterior part of the renal vas deferens near the gonadial duct, which is the functional vesicula seminalis, otherwise the duct was not seen with contents.

There is no open connection between the male genital duct and the pericardial cavity, but a strand of cells connecting the anterior part of the renal vas deferens to the pericardium has been traced in two of the fixed specimens examined. This may indicate the vestige of a gonopericardial duct.

The pallial portion of the vas deferens is glandular and runs alongside the rectum (R) where it can be seen through the body wall in living animals as a slightly coiled chalk-white tube. Near the anterior border of the mantle cavity it enters the penis which, when at rest, lies folded back in the mantle cavity. The posterior part of this pallial duct is a heavily ciliated tube lined by cubical epithelium with large spherical nuclei and, as in the renal vas deferens, there are a few epithelial gland cells of which two kinds can be distinguished. A short duct leaves this posterior part and opens into the mantle cavity on a papilla (AMC). This duct is lined by a uniform cubical epithelium which is heavily ciliated, and its aperture into the mantle cavity is guarded by a sphincter. Some gland cells are also present. The region of the mantle wall immediately behind this opening bears a prominent tuft of cilia.

As the pallial vas deferens passes forwards it widens suddenly to form the most glandular part of the vas deferens, the prostate. Both types of gland cell seen in the previous section are present and are very numerous, occurring in approximately equal numbers. There are no mucous cells. The duct is well ciliated, but the ciliated cells are almost occluded by the many glands. The prostate is surrounded by a well developed muscular coat. The posterior part is coiled, but as it passes forwards it straightens and anteriorly passes into the penis where it narrows, but remains histologically similar. The penial duct (PD) is centrally placed and its aperture (APD) is terminal. Anteriorly it becomes much less glandular and at its extreme anterior end is lined by cubical epithelium only ; it is ciliated throughout its length and is surrounded by a coat of circular muscle. The penis is a muscular organ and even when at rest is nearly as long as the mantle cavity. A strong layer of circular muscle runs immediately below the external epithelium, separated from the similar layer surrounding the penial duct by numerous blood spaces and connective tissue. No gland cells are seen on the surface of the penis.

Only the main features of the female genital system could be discerned in the living animal or by gross dissection, and the details have been obtained from reconstruction of sectioned material.

The ovary (Fig. 1, OV) is a lobulated organ which lies over the digestive gland in the posterior whorls of the body ; in the living animal it can be distin-

guished by the bright yellow globules with which it is filled. In fully mature animals it may exceed the digestive gland in size. The genital duct opens anteriorly into the mantle cavity just in front of the anus (A) near the exhalant siphon (ES) ; this duct is modified to form several distinct organs through which eggs must pass before leaving the body. There are four main glands associated with the female tract ; three of these, the albumen gland (ALG) posteriorly, the capsule gland (CG) and anteriorly a glandular chamber (OD), are all highly specialized regions of the main genital duct ; the fourth gland is the ingesting gland (IG) which opens into this system by its own duct into the region between the albumen and capsule glands.

The ovarian duct (OVD) is short and straight running immediately below the body wall on the columellar side, joining the ovary to the albumen gland. Sperm may be found in large numbers in the albumen gland. In this region the oviduct broadens owing to the glandular nature of its walls and then narrows to form a simple conducting region which passes to the capsule gland. This narrow part comprises a fairly long duct which is coiled at first, but which later curves with the spiral of the animal, immediately below the body wall, and opens ventrally into the capsule gland. The duct from the ingesting gland opens about half way along the duct joining the albumen and capsule glands. The size and condition of the ingesting gland depends on the sexual maturity of the animal and the presence or absence of sperm in the genital system ; in a fertilized animal it is very extensive and ramifies amongst all the adjacent organs in the body cavity ; the duct from the ingesting gland is long and narrow.

There is no trace of a gonopericardial duct in the female. As the posterior end of the heart reaches only about as far back as the end of the capsule gland and lies on the dorsal side of the animal, it is far removed from the renal oviduct and any trace of the gonopericardial connection which may be formed during development is lost.

The lateral walls of the capsule gland are very well developed, but dorsally and ventrally the walls are thinner, so that in transverse section the lumen appears as a dorso-ventral slit. Ventrally the wall of the gland is especially thin and occasionally short ridges of glandular tissue overhang the ventral part of the lumen which, however, is never completely separated from that of the rest of the gland, and the channels do not appear sufficiently well developed to have a marked functional significance. The capsule gland can be divided very roughly into three regions based on the kind of gland cells composing them ; these are dorsally, ventrally and laterally disposed. Anteriorly the capsule gland opens through the ventral part of its lumen into a large distensible vestibule with folded glandular walls which opens directly into the mantle cavity. The opening (FO) is on a papilla which is guarded by a sphincter. There is no vagina or bursa copulatrix. By comparing the length of the undistended penis with the distance from the edge of the mantle cavity of the female, through the female genital pore and the distal glandular part of the oviduct, to the capsule gland, it seems probable that the distended penis can be inserted into the female body at least as far as the capsule gland.

The ovarian duct is comparatively short. It is surrounded by a coat of circular muscle fibres which contract so that the lumen is normally very small.

The epithelium lining the duct is simple, bears no cilia, and there are no gland cells. The duct opens directly into the albumen gland and at this point the surrounding musculature is slightly thickened. The albumen gland is a comparatively small and compact organ surrounded by a coat of circular muscle fibres. Its walls are thrown into deep folds which in unfertilized animals almost occlude the lumen, but when the gland is distended with sperm divide it into numerous compartments. The epithelial cells bear dense, long cilia and are interspersed with numerous gland cells, all of the same kind ; these cells stain deeply with mucicarmine and in some regions of the gland, especially the dorsal wall, are so numerous that the supporting cells between are almost invisible. In fertilized animals large masses of sperm are found in the albumen gland, some of them orientated with their heads embedded in the ciliated cells.

The duct which joins the albumen gland to the capsule gland is surrounded by an extrmely thick layer of circular muscle fibres, which are especially dense at the junction with the capsule gland. Posteriorly the duct is coiled. Its lumen is lined by a single layer of epithelial cells bearing cilia and there are no gland cells. It may contain sperm, which in the posterior part before the opening of the duct into the ingesting gland are orientated. The duct to the ingesting gland opens into the anterior half of the duct joining the albumen and capsule glands and is guarded by a sphincter; the duct is long and straight and surrounded by a very thick layer of circular muscle ; there are no cilia or gland cells ; sperm, many of which are orientated, may be found in the duct.

The ingesting gland is branched, each tubule being lined by a single layer of cells ; all the cells are similar, but their condition at any one time is variable. In a fertilized animal the lumen of the ingesting gland is filled with sperm, many of them arranged in large bundles with their heads embedded in the cells of the gland. In other gland cells small groups of elongated granules showing outlines which resemble sperm heads are seen and these appear to be partially digested sperm. Other groups of smaller granules which stain in the same way as the absorbed sperm and the partially digested sperm can be seen in the cells of the gland and may be part of the same process. No cilia are seen in any part of the ingesting gland. The whole gland is enclosed in a thin muscular coat.

Three different kinds of gland cell can be distinguished in the capsule gland, each localized in one or more parts of the gland, thus dividing it into regions. The most numerous kind is found in the median region of each lateral wall in elongated clusters surrounding a central narrow duct leading to the main lumen of the gland ; each cluster is bound by a thin layer of connective tissue which is continuous with that binding neighbouring clusters. Each gland cell has a basal nucleus and is full of large protein granules. Between these clusters of gland cells are supporting cells bearing dense, long cilia. At the anterior and posterior ends of the capsule gland the extent of this kind of gland cell is much reduced. In the dorsal and dorso-lateral regions the cells are not arranged in clusters but lie in a single layer on the basement membrane with small supporting cells between them bearing cilia. These gland cells are very elongated and are filled with irregularly shaped granules of moderate size. Posteriorly

these gland cells spread laterally and replace the median region of deeply staining clustered cells, and at the extreme posterior end of the capsule gland extend almost to the ventral channel. Anteriorly these cells are slightly separated from the adjacent glandular areas by a slight folding in the wall of the capsule gland. The gland cells of the ventral region spread laterally to occupy almost the whole of the anterior region of the capsule gland, but more posteriorly they gradually become confined to the ventro-lateral walls on either side of the ventral channel, and at the posterior end of the gland are represented by two thin strips of gland cells only. The cells are arranged in a single layer on the basement membrane and are interspersed with very small cells bearing short celia. The granules in these cells are very small and respond to stains for mucus.

The ventral channel itself is not glandular but is lined by a single layer of very small cells which bear no cilia ; the channel, however, is overlapped by cilia present in the glandular regions on either side of the channel. At the anterior end of the capsule gland the glandular wall bordering the ventral channel becomes folded to form an anterior projection which extends into the next region of the genital system, into which the capsule gland opens.

The whole of the capsule gland is sheathed in a muscular coat which lies immediately below the basement membrane but does not extend up with the membrane between the clusters of gland cells, it is thickest below the posterior part of the ventral channel ; in other regions its thickness seems fairly uniform.

The distal portion of the oviduct is a large sac lying under the anterior part of the wall of the mantle cavity ; its walls are folded longitudinally and are extremely glandular. It is enclosed in a muscular coat and is lined by a single layer of cells most of which are gland cells interspersed with ciliated cells. There is no sign of a bursa copulatrix. The duct opens into the mantle cavity at its anterior end on a short papilla.

DISCUSSION

The anatomy of the gut of such animals as the toxoglossan prosobranchs has naturally been the subject of investigation and Bouvier (1887), Amaudrut (1898) and Shaw (1914) have described the gut in a variety of species of conids. Our knowledge of the feeding methods of these animals was until recently mainly based on the work of Alpers (1931) but has been greatly extended by observations made by Kohn (1956, 1959) in Hawaii, where a numerous population of conids exists. Some of these eat worms, others eat molluscs and still others fish. In some vermivorous forms the proboscis, holding a tooth at the apex, is extended to ' sting ' the prey ; the proboscis is then retracted, leaving the tooth embedded in the body of the prey, which is anaesthetized and swallowed at leisure. In other species the mollusc does not lose its grip on the prey by separation of the tooth and contraction of the proboscis therefore draws the immobilized prey towards it. In all cases the mouth appears capable of enormous dilation and the body of the prey is ingested whole.

In *Mangelia* the retracted proboscis is exceedingly long. I have not observed it evaginated, but the nature of the musculature and the length of the poison gland suggest that its everted length may be very considerable. It has already

been noted that *Mangelia* possesses no sucker such as that found on the sole of the foot of *Nucella lapillus* (Fretter, 1946), to which an accessory function during feeding is ascribed. Its absence may link with the fact that ingestion of food takes place some distance from the foot or, if the views of Carriker (1955) are right, that no boring of prey occurs, or both. The supporting sheath, however, may enclose the everted proboscis to strenthen and support it, and the double sheath at its anterior end is also capable of forming a stabiliser. The proboscis, therefore, whilst pleurembolic like that of the Rachiglossa, differs in that the cavity in which its base lies is permanent and is never everted.

The idea that the extended proboscis is extremely long rests on the fact that the poison gland (the 'duct' of earlier authors) lies folded freely in the body cavity and, in the absence of observations of the action of the proboscis, it seems reasonable to postulate an extension of the buccal tube compatible with its straightening. The other appendages of the buccal tube are the radular sac and the salivary glands. The radular sac is attached to the body wall by extensible muscle fibres and the salivary glands lie freely in the body cavity, offering no resistance to extension of the tube. The disposition of the cells lining the buccal cavity when the proboscis is retracted, and the extremely muscular nature of its walls, suggest that the buccal cavity can extend sufficiently to keep up with elongation of the proboscis to the degree that the length of the poison gland suggests, whilst the nerve ring is wide and can accommodate the radular sac and salivary glands when required. The disposition of these organs is similar to that described for *Conus vicarius* (Amaudrut, 1898), and for *C. tupila* and *C. textile* by Shaw (1914) except that in the last two species the salivary glands form a single mass provided with two ducts.

It has been suggested, however (Alpers, 1931), that the proboscis of the Toxoglossa is not protrusible, and that the exposure of the oral disc is achieved by retraction of the sheath and even part of the proboscis wall, so that the buccal tube is everted and a 'mouth' formed at the level where radular sac, poison gland and salivary gland open. In this case the poison gland will remain coiled more or less to the same extent whatever the condition of the proboscis, and its length will not be needed to provide slack to be taken up when the proboscis extends. Its shape, indeed, may simply represent the only way in which adequate secretory surface can be obtained in a gland which has to be linear in form because its secretion is ejected by pressure from a muscular bulb at its innermost end. In all the (fixed) specimens of *Mangelia* which I have observed, the proboscis, although found in different positions in relation to its sac, always retains the same form with a marked oral structure terminally.

In most prosobranchs, including the rachiglossan Stenoglossa, the gut anterior to the stomach can be divided into a buccal cavity and an oesophagus showing a glandular middle section between anterior and posterior parts not especially so. In the Rachiglossa the mid-oesophagus has been highly modified (Graham, 1941) and the glandular part stripped from the main channel to form the gland of Leiblein, the site of the separation being marked by an excessively thin streak on its morphologically ventral wall ; in addition, its most anterior part has enlarged to form a bulbous valve known as the pharnyx of Leiblein. In mesogastropods the whole of this part of the oesophagus lies posterior to

the nerve ring, but in Rachiglossa—presumably as a consequence of the formation of the proboscis—the anterior part of the mid-oesophagus which forms the pharynx of Leiblein has passed forward through the nerve ring, though the gland of Leiblein and its duct are still behind it.

The alimentary canal anterior to the stomach in the Toxoglossa is clearly divisible into two regions only ; the buccal cavity and the oesophagus, but these two regions cannot correspond to the structures of the same name in the Rachiglossa.

The buccal cavity in *Mangelia* receives the openings of the buccal sac and the poison gland and extends from the mouth to the sphincter which separates it from the oesophagus just anterior to the nerve ring. This prevents food from being sucked forwards when the proboscis is rapidly extended and corresponds in position and function with the pharynx of Leiblein in the Muricacea. The oesophagus is most similar in anatomy and histology to the posterior oesophagus of a rachiglossan, so that at first sight it would seem that the sphincter is the only structure which remains of the mid-oesophagus of these animals. In so far as it retains a pad of ciliated and mucous cells it probably represents the vestiges of the pharynx of Leiblein.

It has, however, been suggested (Amaudrut, 1898) that the poison gland is derived from the gland of Leiblein, which is homologous with the oesophageal glands of lower prosobranchs, though in *Mangelia* it appears to connect to the buccal cavity, and this homology is implicitly accepted by Shaw (1914). In the former this is the region affected by torsion, whereas in *Mangelia* the arrangement of the salivary ducts show that this is the region of the alimentary canal which has been invovled. Since these are appendages of the buccal cavity, this fact gives an indication that the mid-oesophageal region in the Toxoglossa is not only reduced but practically absent and that the use of the terms ' buccal cavity ' and ' oesophagus ' is not in conformity with normal prosobranch usage. The poison duct opens anterior to the sphincter although most of the gland and its muscular bulb lie posterior to it, and the whole is anterior to the nerve ring. In the Rachiglossa the gland of Leiblein and its duct lie posterior to the nerve ring, although derived in part from the pharynx of Leiblein which is anterior to it. The same traction exercised by a proboscis which pulled the pharynx of Leiblein through the nerve ring could conceivably cause the gland of Leiblein and its duct to do likewise, and so produce a gland wholly anterior as the poison gland and the sphincter of Toxoglossa are. However this would not account for the fact that the poison duct opens anterior to the sphincter which is believed to replace the pharynx of Leiblein. Amaudrut (1898) accounted for this by supposing that, whereas in the Rachiglossa the gland of Leiblein had been stripped from the oesophagus from before backwards, in the Toxoglossa the glandular tissue was stripped from the oesophagus from behind forwards, though the presence of a morphological ventral streak in the oesophagus of the Toxoglossa marking the site from which the glandular material has been stripped cannot be demonstrated. This may be due to the extreme specialization and reduction of the mid-oesophageal region in these animals, since even in Rachiglossa it is all but invisible in *Nassarius reticulatus* (Graham, 1941). This theory would explain the difference between

the relationship of the opening of the ducts to the nerve ring in the two tribes. In the Buccinacea Graham (1941) describes how the blind end of the gland of Leiblein tends to become non-glandular. In the Toxoglossa this tendency might not be associated with the reduction of the gland, but might precede the development of a terminal muscular propulsive organ.

Graham (1941) offered an alternative homology by comparing the ventral salivary glands found in *Nucella* and *Ocenebra* with the poison gland of *Conus*, the gland cells of both organs being histologically similar. Since he could find neither amylolytic nor proteolytic enzymes in the ventral salivary glands, a digestive function for these glands appears to be precluded, though they may help in boring the shells of these animals' prey. Their extract does not appear to have a toxic effect, but the action of a poison would not be important in the feeding of these animals. Franc (1952a & b) observes that the ventral or accessory salivary glands give a positive reaction for phosphatase as does the gland of Leiblein ; but on the other hand no reaction is obtained from the poison gland of *Philbertia purpurea*. Again, this does not necessarily exclude the validity of the homology of the two glands, especially as it is not clear what structure Franc was dealing with under the heading poison ' gland '.

The disposition of the ventral salivary glands is similar to that of the poison gland, and the fact that the gland is surrounded by a muscular coat suggests that the derivation of the poison gland with its terminal muscular bulb is simply a matter of localization of the muscular and secretory parts of the gland to the proximal and distal regions respectively, with subsequent enlargement of the muscular region to form a powerful bulb. Such a derivation would also involve postulating the backward migration of the single ventral opening of the gland from the ventral lip to the ventral region immediately posterior to the opening of the radular sac, and either the fusion of the paired glands or the suppression of one of them.

As far as I can discover, Hermitte (1946) is the first to distinguish the poison apparatus of *Conus* as a tubular gland terminated posteriorly by a blind muscular bulb, and concludes that the so-called poison sac is solely a storage and propulsive organ and that the so-called poison duct of Amaudrut and others is in fact the poison gland.

From its anatomy and from comparison with the Conidae it seems that *Mangelia* is undoubtedly a predatory carnivore of a highly specialized kind. In other Toxoglossa the venom has a powerful neurotoxic action and that of *Mangelia* is probably similar but the prey in unknown. As shown by Alpers (1931) and Kohn (1956, 1959) *Conus* spp. swallow the prey whole, and since the injecting mechanism in *Mangelia* is powerful and its store of venom large it is possible that its prey is limited by what is available in the environment and the extent of accommodation afforded by its gut. Since the mouth lies at the centre of a sucker it is likely that *Mangelia* never loses its grip on the prey after it has been ' stung '. Alternatively this might indicate that *Mangelia* differs from the cones in not ingesting its prey whole but in immobilizing it by means of its venom and then sucking fluid from it.

The male genital duct of *Mangelia* shows no distinction of the pallial vas deferens into a prostate, although there are gland cells which are more numerous

in the proximal regions of this duct. The pallial vas deferens runs below a ridge on the body wall and is separated from the other structures in the body cavity by a muscular septum ; this is the only indication that this region may once have been associated with the mantle cavity. The accessory opening to the mantle cavity is well marked at the end of a short duct leading from the posterior end of the pallial vas deferens ; it resembles the structure found in *Nassarius* and *Buccinum* ; it is clearly an integral part of the male genital system and probably acts as a safety valve in the same way as has been suggested for *Buccinum*. Traces of the gonopericardial duct remain as a thin strand of connective tissue.

The female genital duct can be referred to the same basic plan attributed by Fretter (1941) to the genital ducts of the Mesogastropoda and Stenoglossa. A narrow oviduct leads to a glandular distal section. The gonopericardial duct which opens from the juncture of these two regions and leads to the pericardium is not found in *Mangelia*. Its absence most probably results from the fact that this region of the genital duct is far removed from the heart and the function of the duct in the Stenoglossa appears to be a negative one. The ingesting gland in *Mangelia* can be extremely large, and, as in other Stenoglossa, occurs in a similar relative position to the receptaculum seminis of the Mesogastropoda, and is probably homologous with it. It is undoubtedly an absorbtive organ but certain regions also act as a storage place for sperm. The formation of the capsule gland from an open groove, with the lateral walls thickened by gland cells, and the ventral edges fused to form a closed duct, is apparent. The ventral channel, formed, presumably, at the point of closure, is simple in *Mangelia* and no longitudinal fold separates it from the lumen of the gland, as in rachiglossans such as *Buccinum* and *Nucella*, in which the channel is a passage for sperm. This feature may be associated with the absence of a bursa and the size of the penis. The penis is extremely long and probably penetrates the genital duct passing along the ventral channel to the proximal end of the capsule gland or beyond, depositing the sperm directly in the proximal part of the genital duct in the same way that sperm are deposited directly in the receptaculum which lies in a similar position in some other forms. Sperm may be stored in the ingesting gland or in the albumen gland.

There is no ventral pedal gland in either male or female *Mangelia* ; it is possible however that the extremely muscular walls of the vestibule play some part in moulding the egg capsule as it passes to the exterior. No observations have been made on the egg capsule or the development. Lebour (1937) describes the egg capsule of *M. nebula* as smooth and does not remark on any difference in its appearance from those of other Stenoglossa which have been moulded by a ventral pedal gland. The tendency for the suppression of the free-living larva shown in the Stenoglossa does not appear to extend at least to this representative of the Toxoglossa ; the young hatch as free-living veligers with a relatively long planktonic life (Lebour, 1937).

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THE GENITAL SYSTEMS OF THE FRESHWATER BASOMMATOPHORA

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(With 8 figures in the text)

Following a comparative histological investigation of the genital systems of representatives of the four families of the Hygrophila, a standardized nomenclature for the different parts of the female duct is proposed and homologies are suggested.

The reproductive systems of *Physa fontinalis*, *Lymnaea peregra*, *Planorbarius corneus* and *Ancylus fluviatilis* are described and all four species differ in the relationship of the fertilization pockets to the union of hermaphrodite, male and female ducts. In the Physidae alone, the ova pass into the albumen gland and there is no albumen gland duct, a condition which is similar to that of *Succinea*.

The Chilinidae probably stand close to the ancestral condition of the Hygrophila and the prostatic histology of *Chilina* resembles that of the Physidae, Ancylidae and Planorbidae, whilst the cells of the prostate of the Lymnaeidae are fundamentally different.

The degree of development of the different parts of the oviduct in the four families is illustrated. Oviduct I is a short conduit and oviduct II, which is extensively developed in *Physa* and *Lymnaea*, is comparable to the posterior portion of the female tract of *Chilina robustior*. In oviduct III the fertilised ova are embedded in viscous fluid and enclosed in the capsular membrane and this region of the female duct becomes greatly folded in the Lymnaeidae and Planorbidae to form the oothecal gland. Oviduct III is absent in *Ancylus* where oviduct I opens directly into oviduct IV, a region which has a specialized histology. Oviduct IV is also found in *Planorbarius*, following oviduct III, and is therefore a common feature of these two families.

It is concluded that the genital system of the Physidae is nearest to the ancestral condition, from which the Planorbidae and Ancylidae are later offshoots. The reproductive system of the Lymnaeidae, while retaining several features in common with that of the Physidae, has probably followed a separate evolutionary path.

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INTRODUCTION

In a previous publication the evolution of the pulmonate genital system was traced and it was suggested that the arrangement and structure of the reproductive organs found in the Chilinidae represent a prototype from which a generalized member of the Hygrophila (the freshwater families of the Basommatophora) may be derived (Duncan, 1960a). In the present account the evolution of the genital system within the Hygrophila is discussed.

Hubendick (1947) has given a comprehensive description of the phylogenetic relationships between the four families of the Hygrophila, but considers that of the reproductive organs only the prostate and penis present fundamental differences within the group. There have been several accounts of the anatomy of the reproductive systems of a number of pulmonates, but considerable confusion exists in the nomenclature used to describe the various organs, especially those of the female tract. The terminology proposed for the genital system of *Physa fontinalis* (Duncan, 1958) is therefore followed in the present account. Representatives of the Lymnaeidae, Planorbidae and Ancylidae have been studied, using the same histological techniques as was used for *Physa*, and a brief description of the genital tracts is given. The comparative arrangement of the component organs is shown diagrammatically in Fig. 1. The same pattern of organization can be distinguished in all four families and only those features of interest will be described in each representative, *Physa fontinalis*, *Planorbarius corneus*, *Lymnaea stagnalis* and *Ancylus fluviatilis*. The classification and nomenclature given in the " Census of the distribution of British non-marine Mollusca " (Ellis, 1951) have been followed for the British species mentioned.

METHODS

Snails were dissected in a saline medium isotonic with the blood of *Lymnaea stagnalis* and usually fixed in Susa. Transverse and longitudinal sections were cut at 6 and 8 μ and stained with Heidenhains azan or iron haematoxylin.

THE PHYSIDAE

The reproductive system of *Physa fontinalis* has been described in greater detail elsewhere (Duncan, 1958 and '59) and is illustrated diagrammatically in Figs. 1A and 2. Both sperm and ova are formed in the ovotestis and then pass down the common hermaphrodite duct to the point where the male and female systems separate. The spermatozoa travel to the penis via the vas deferens. In the proximal part of the vas deferens the prostatic secretion is added ; in the Physidae the prostate follicles are numerous, blind finger-like diverticula which frequently branch at the base.

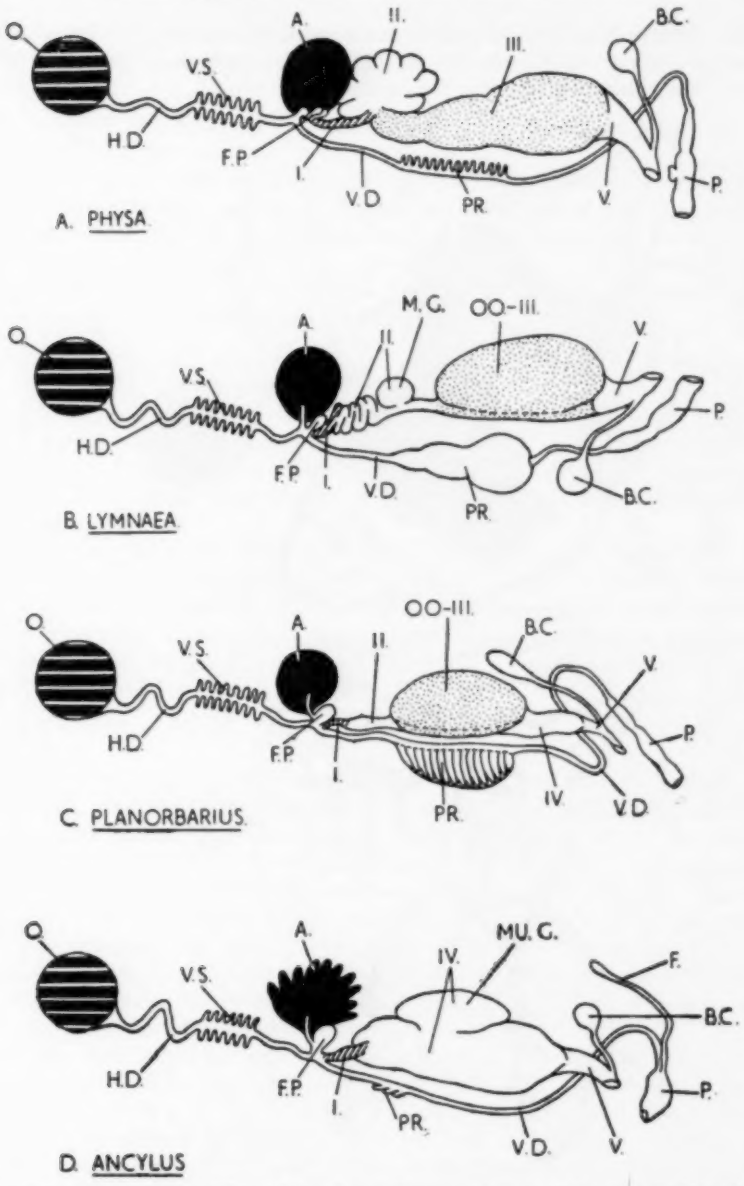

Fig. 1.—Comparison between the genital systems of representatives of the four families of the Hygrophila.

(A) *Physa fontinalis* ; (B) *Lymnaea peregra* ; (C) *Planorbarius corneus* ; (D) *Ancylus fluviatilis*.

A., albumen gland ; B.C., bursa copulatrix ; F., flagellum ; F.P., fertilization pocket ; H.D., hermaphrodite duct ; M.G., muciparous gland ; MU.G., mucus gland ; O., ovotestis ; OO-III, oothecal gland, oviduct III ; P., penial complex ; PR., prostate ; V., vagina ; V.D., vas deferens ; V.S., vesicula seminales ; I, II, III, and IV, oviducts I, II, III and IV.

The female tract is subdivided into a posterior, glandular oviduct and a muscular vagina which opens to the exterior at the female aperture. Three regions are distinguishable in the oviduct :—

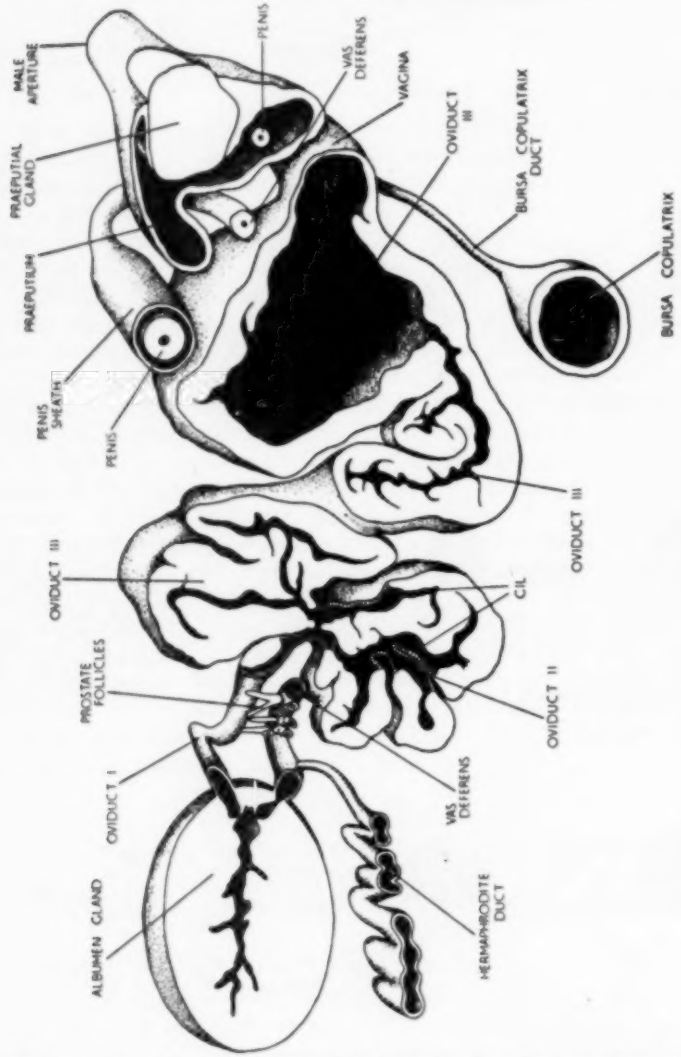

Fig. 2.—*Physa fontinalis*. Diagrammatic stereogram showing structure and arrangement of the genital ducts, viewed from the right-hand side. Ovotestis omitted. CIL., tracts of cuboidal, ciliated cells.

Oviduct I is a short, narrow conduit leading to the junctions of oviducts II and III. The characteristic columnar, secretory cells are closely packed together, but immediately before this part of the duct joins oviduct II a ciliated tract of low cuboidal cells is developed and this unites with a similar epithelium in oviduct II (see Fig. 2).

Oviduct II is a much convoluted diverticulum of the female tract in which the ciliated epithelium is extensively developed in addition to the columnar, glandular cells.

Oviduct III, the major part of the female duct, is swollen when mature and is formed of the columnar secretory cells.

Two accessory organs are associated with the female tract ; the albumen gland, standing at the junction of the hermaphrodite duct with the oviduct and vas deferens, produces the nutrient medium which surrounds the fertilised ova, whilst the bursa copulatrix is a diverticulum for the storage of foreign sperm, the duct of which opens into the vagina. Both these accessory organs have a similar histological structure throughout the Hygrophila.

THE LYMNAEIDAE

Crabb (1927 a, b), Holm (1946) and Bretschneider (1948 a, b) have given detailed accounts of the histology and functional morphology of the reproductive system of *Lymnaea stagnalis* and the brief description of the anatomy of the genital tract of *L. peregra* which follows is correlated with this existing knowledge.

Fig. 1*b* illustrates the general plan of the reproductive organs and the differences between it and the condition in the Physidae will be appreciated. These may be summarized by saying that the prostate consists of an inflation of the vas deferens and in the female tract there is an additional organ, the muciparous gland, whilst distally the oviduct is enormously swollen to form the oothecal gland.

The female system

Oviduct I is a short, non-convoluted duct which is formed initially of ciliated cells, identical with those of the albumen gland duct, but which are subsequently replaced by elongated cells with basal nuclei whose cytoplasm stains deep blue after azan. Oviduct I merges into oviduct II, whose convolutions pass around the longitudinal axis of the genital system (see Fig. 3), before receiving the opening of the muciparous gland. As in *Physa* spp., the wall is composed of cells of two types, (*a*) Tracts of columnar, ciliated cells, amongst which are interspersed a few goblet cells, and (*b*) Glandular cells which comprise the remainder of oviduct II. Wedged between the apices of these are the characteristic ciliated interstitial cells.

Towards the end of its convolutions, oviduct II receives the opening of the muciparous gland, but there is no true duct, the gland being closely adposed to the surface of the oviduct, of which it is little more than a blind diverticulum of similar histological structure. It is therefore regarded as being part of oviduct II. The walls of the muciparous gland are highly folded and composed of columnar, mucus-secreting cells, and wedged between the apices of these are the usual ciliated cells.

The oviduct finally runs anteriorly and merges into the oothecal gland (Holm's nomenclature), which is very swollen (Fig. 4) and corresponds to oviduct III. Internally the wall is intricately plicated and the follicles so

formed have their walls composed of cells identical with those found in the muciparous gland, although the complex follicular arrangement gives the organ a totally different appearance. The ciliated tract of the upper portion of the oviduct is continued as a small gutter along one side of the organ, but

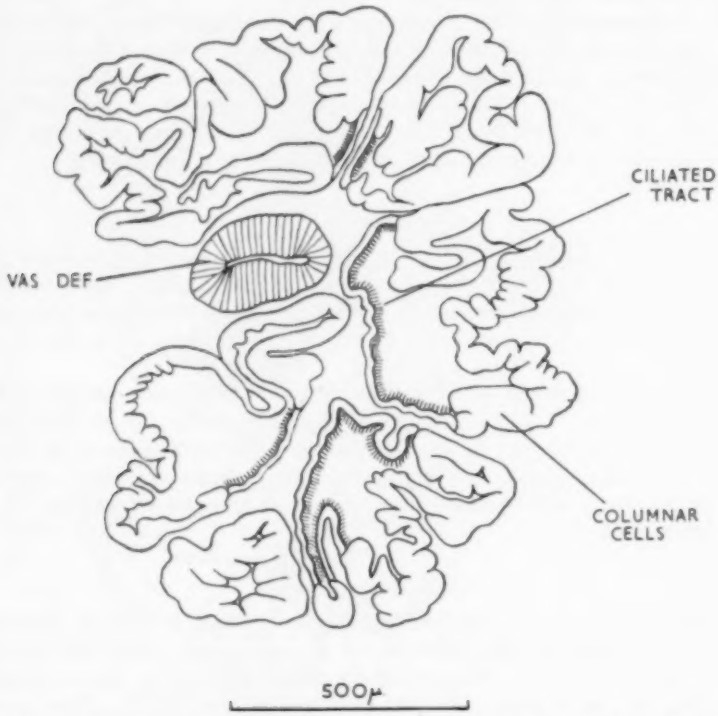

Fig. 3.—*Lymnaea peregra*. Diagrammatic transverse section of the convolutions of oviduct II around the vas deferens.

neither it nor the muciparous gland has its counterpart in the Physidae. The ciliated gutter becomes confluent with the cuboidal cells of the vagina, into which the oothecal gland finally merges.

The male system

On separating from the hermaphrodite duct, the vas deferens passes into the prostate in which two zones can be differentiated externally :—

(*a*) Upper, non-bulbar portion. A simple duct whose columnar cells have a basal nucleus and are packed with brown granules, when stained with azan. There is a gradual transition into :—

(*b*) Lower bulbar region, where the surface of the inner face of the gland is increased by large infoldings. As one passes anteriorly, the staining reaction of the component cells undergoes regular changes. Initially, the cytoplasm is formed of the brown granules found in the non-bulbar portion but this region is replaced by a band of cells staining

bluish-purple with azan. More anteriorly, the prostatic cells stain blue, but small segments of the wall in this portion are coloured yellow and bright red. The cells here are elongated and compressed, in contrast to those at the proximal end of the male tract where they are shorter.

No ciliary currents have been described in the prostate of *L. stagnalis*. In both this species and *L. peregra*, however, when living tissue is examined, ciliated cells can be seen in this organ. In fixed preparations these appear as small, wedge-shaped cells, found between the apices of the glandular cells and comparable with those in the prostate of *Physa* spp. Otherwise the prostatic histology is in marked contrast to that of the Physidae (see Hubendick, 1947).

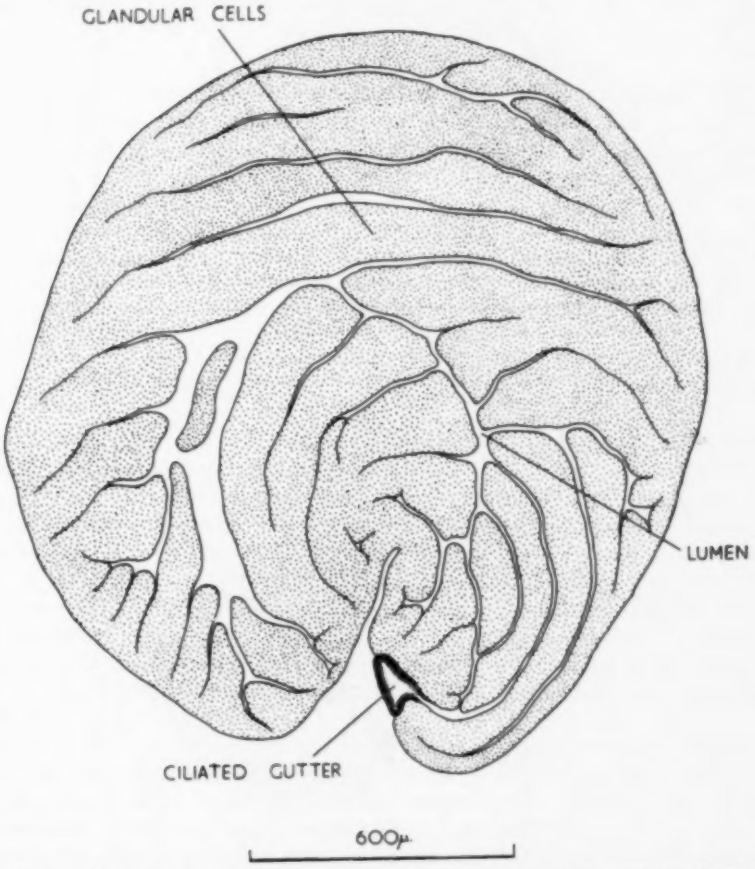

Fig. 4.—*Lymnaea peregra*. Diagrammatic transverse section of the oothecal gland.

THE PLANORBIDAE

In 1863 Baudelot described and figured the morphology of the genital system of *Planorbarius corneus* and Baker (1945) has given an extensive survey

of the family Planorbidae and this contains morphological accounts of the reproductive system of many species. Hubendick (1955) has discussed the phylogeny of the family and Abdel-Malek (1954 a, b) has described the genital organs of *Helisoma trivolvis* and *Biomphalaria boissyi*.

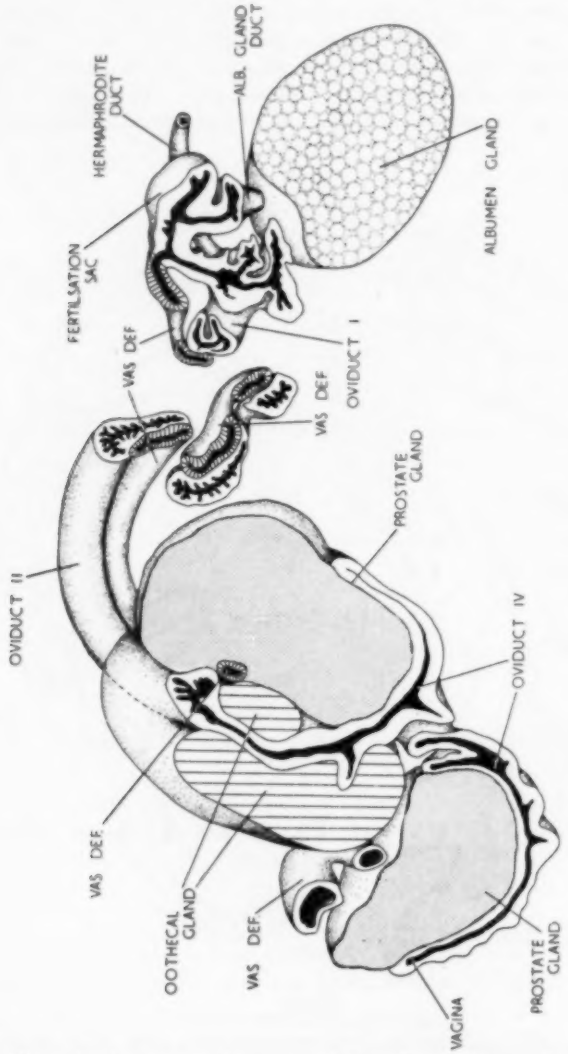

Fig. 5.—*Planorbarius corneus*. Diagrammatic stereogram of a longitudinal section of the genital ducts, viewed from the left-hand side. Ovotestis omitted.

When *Planorbarius corneus* is removed from its shell, uncoiled and dissected, the genitalia are seen to be long and attenuated and the general arrangement is shown in Figs. 1C and 5. The basommatophoran design is evident in spite of the elongated form. Of note is the intimate association between the male

and female systems, the vas deferens being embedded in the surface of the large oothecal gland whilst the oviduct passes directly through the prostate. This latter organ is formed of follicles enclosed within a common membrane. There is no muciparous gland.

The albumen gland is typical in its histological structure. Immature specimens show the usual gradation of increasing cellular activity passing from the periphery to the centre of the gland. Like the Lymnaeidae, the central lumen is lined by ciliated cells on one face only, the opposite side having glandular cells opening directly into the cavity. The albumen gland duct, however, is completely ciliated and closely resembles the fertilization sac which is lined by columnar, ciliated cells (see Fig. 8).

The female system

There is the usual differentiation into regions in the female duct, oviduct I being short and composed of ciliated cells which usually fail to stain with azan. By a gradual transition in its histology it merges into oviduct II which initially is twisted and convoluted but later follows a straighter course. Its wall is formed of bands of cells of two types :—

(*a*) Tracts of columnar, secretory cells with colourless cytoplasm, between which are swollen, flask-shaped cells with granular contents. The latter usually stain a deep blue with azan, but cells which have yet to reach secretory activity are coloured red, whilst an intermediate condition is also found, the cytoplasm staining red basally and blue apically. Inserted between the cell apices are wedge-shaped, ciliated cells (see Fig. 6).

(*b*) Bands of ciliated cells comprise the remainder of oviduct II. Glandular cells are scattered at intervals amongst the ciliated cells and are flask-shaped and packed with blue-staining granules.

Gradually all the glandular cells are lost and the completely ciliated oviduct merges into the oothecal gland and continues within it as a ciliated gutter, lying on one side of the organ and receiving the secretory products. The histology also corresponds to the oothecal gland of *Lymnaea*. Thus, the glandular cells are arranged in a series of follicles and diverticula, producing a greater surface area and a corresponding increase in secretory capacity. The cells are columnar and swollen, with tetrahedral, ciliated cells inserted between the cell apices. The evaginations and follicles of the gland form a branching system, with collecting ducts which open into the main channel, the continuation of the ciliated groove. The latter becomes glandular and re-emerges as oviduct IV (Fig. 5).

Oviduct IV, which has no counterpart in the Physidae and Lymnaeidae, runs from the dorsal side of the genital system, where it originates, and passes through the prostate, re-emerging on the ventral side. The walls are formed of glandular cells which stain deeply and are packed with secretory material. At maturity the cytoplasm is granular, some cells being packed with granules and globules which stain dark red after azan, while others appear blue. These are probably two different phases in the secretory cycle, since intermediate conditions were found. Part of the periphery of the lumen, however, is lined by a band of ciliated, cuboidal or columnar cells and the usual ciliated cells were found between the cell apices of the glandular tract.

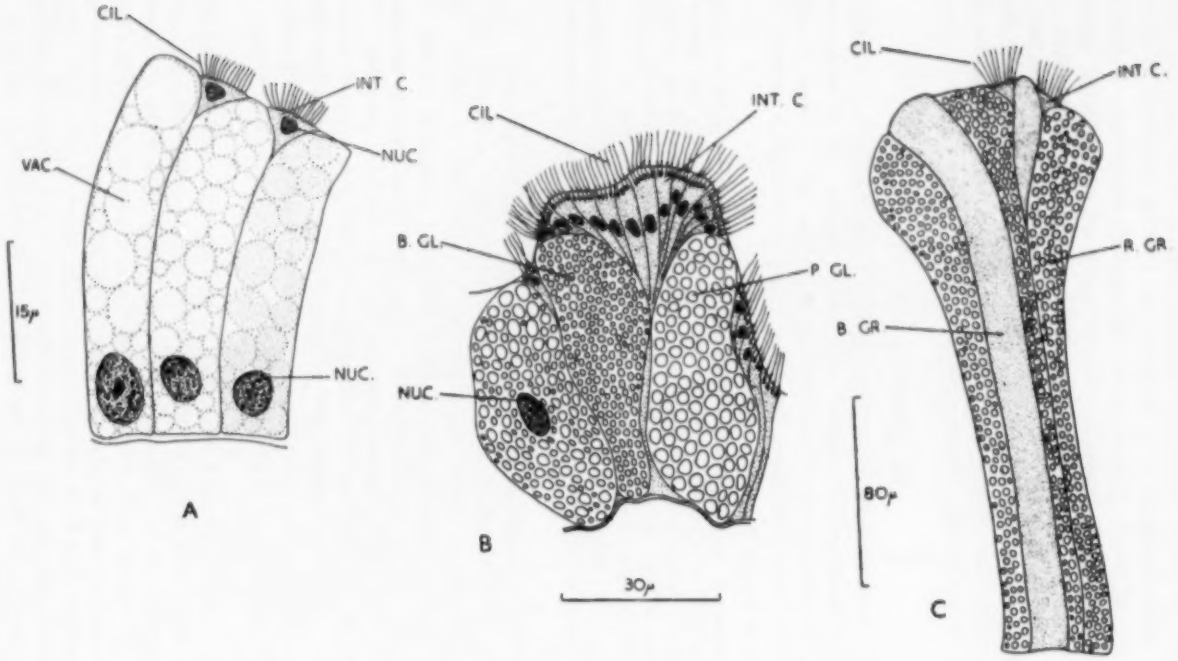

Fig. 6.—*Planorbarius corneus*. Secretory cells of the female system. Fixed susa, stained azan.
(A) Oothecal gland ; (B.) Oviduct II ; (C) Oviduct IV.
B.GL., blue staining globules ; B.GR., blue staining granules ; CIL., cilia ; INT.C., interstitial cell ; NUC., nucleus ; P.GL., purple staining globule ; R.GR., red staining granule ; VAC., vacuole.

The duct of the bursa copulatrix is ciliated, although nearer the organ itself, the cilia are lost. Abdel-Malek (1954 a, b) reports a similar condition in *Helisoma* and *Biomphalaria*, and the Planorbidae appear to differ from the other three families in this respect.

The male system

The vas deferens follows a tortuous path until it becomes embedded on the face of the oothecal gland. The prostate is also closely adposed to one face of the oothecal gland and the male duct passes into it and comes to resemble one of the prostatic follicles. The vas deferens is formed of columnar cells which are filled apically with globules which stain blue after azan, whilst basally they are packed with purple granules and vacuoles are often present in this lower portion of the cells. At the peak of activity, the whole cell is filled with blue-staining globules. Interstitial ciliated cells are present (Fig. 7).

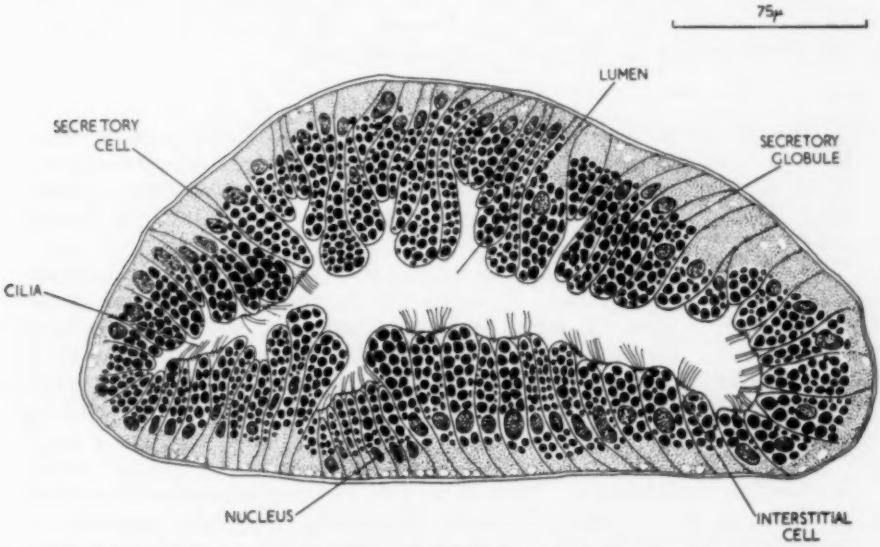

Fig. 7.—*Planorbarius corneus*. Transverse section of the vas deferens, proximal to the prostate.

The prostate is formed of follicles which open into a series of collecting ducts and, although they are contained in a common envelope, the histology closely resembles that found in *Physa* (see Duncan, 1958). The collecting ducts have a similar histological structure and open into the vas deferens, which at this point becomes muscularized and changes in histology, being formed of columnar, ciliated cells.

THE ANCYLIDAE

In 1899 Lacaze-Duthiers described the anatomy of the reproductive system of *Ancylus fluviatilis* and his account formed a basis for the present

investigation. Since then, Hoff (1940), working on *Ferrissia tarda*, has described the morphology of the reproductive system and Basch (1959) has given an account of the anatomy of *Laevapex fuscus*.

The plan of the genital system of *Ancylus fluviatilis* is shown in Fig. 1D ; the ovotestis is less branched than in other basommatophoran families, whereas the albumen gland is a lobulated organ. The prostate is reduced to three follicles, but the male system has an accessory organ, the flagellum, a long, blind duct which enters the penis beside the vas deferens. The fertilization sac is conspicuously situated at the separation of the male and female tracts.

The hermaphrodite system

Hoff (1940) records that the ovotestis of *Ferrissia* is roughly spheroidal and this tendency towards simplicity of gonad form is found in *A. fluviatilis*. In *Laevapex* it is hemispherical and divided into about 20 follicles (Basch, 1959). In the hermaphrodite duct, glandular pockets are found, but the vesicula seminales are not as well developed as in other families and Hoff records a solitary storage vesicle in *Ferrissia*. Basch, however, reports that the storage vesicle in *Laevapex* is enormously dilated.

The female system

The digitate albumen gland is composed of large follicles, each of which has a spacious, central lumen, the follicular canals uniting and leading directly to the albumen gland duct which is short and composed of collumnar, ciliated cells. In *Laevapex*, the albumen gland is a flat, ribbon-like body (Basch, 1959).

Oviduct I leaves the fertilization sac and is a short, communicating conduit with a small, central lumen. It opens directly into the main region of the female duct, oviduct IV, which is a convoluted tube with a large lumen. Histologically, the component cells resemble those of oviduct IV of *Planorbarius*. Cells packed with bright blue globules after azan alternate with those filled with pale blue contents, but tracts containing the characteristic bright red droplets are found.

The ' mucus gland ' is a large convoluted evagination of oviduct IV which it resembles histologically. There is no duct to the gland and it is regarded as belonging to this part of the female system. Nothing comparable to oviducts II and III in the Physidae and Lymnaeidae is found in *Ancylus fluviatilis*.

The male system

The vas deferens is formed of columnar cells with a large, basal nucleus and filled with secretory globules. After azan, most of these stain blue, although a few cells filled with orange granules can be found. Tetrahedral, ciliated cells are placed interstitially. The three prostate follicles and the flagellum present a similar histological picture and therefore resemble the prostate found in the Physidae. Both the vas deferens and the flagellum become muscularized at their lower ends, the former passing through the mantle wall before both enter the penial complex together. Seven to nine

prostatic follicles folded over upon themselves are reported in *Laevapex* (Basch, 1959) and the resulting prostate is relatively large ; the flagellum, however, is absent in this genus. In *Ferrissia* the prostate is an oval body, through which the vas deferens makes a coiled loop (Hoff, 1940).

DISCUSSION

Hermaphrodite system

The ovotestis, hermaphrodite duct and vesiculae seminales have a common morphological and histological appearance in all the representatives studied, but at the union of male, female and hermaphrodite ducts, each family has a characteristic arrangement which is shown diagrammatically in Fig. 8. In the primitive pulmonates a fertilization pocket is found associated with the albumen gland (Duncan, 1960 a) and this sac persists in all four families of the Hygrophila, although they differ in the point at which it opens into the genital system. The albumen gland is composed of characteristic secretory cells, although in the Ancylidae the gland is prolonged into digitations or becomes ribbon-like. Usually the albumen gland duct opens at the point of union of the genital ducts, but in *Physa* the albumen gland duct is absent and the male and female systems fuse within the body of the albumen gland. Thus, in the Physidae (see Fig. 8) the hermaphrodite duct joins the upper end of the vas deferens and the ova pass into the albumen gland, receiving the secretion of galactogen, and so continue into the oviduct (Duncan, 1958). There is an essential similarity to the arrangement in *Succinea* (Duncan, 1960 b). In *Physa*, two or three fertilization pockets open into the first portion of oviduct I, although this is probably not the site of fertilization. The ova are generally fertilized at the lower end of the hermaphrodite duct.

The hermaphrodite duct of *Lymnaea peregra* opens into a cavity formed at the confluence of the male and female systems (Fig. 8 b). In this species there is a single fertilization pocket which joins this union of the three genital tracts. The albumen gland is separate and its duct opens at the base of the fertilization pocket.

A feature common to all members of the Planorbidae so far studied is the large fertilization pocket. In *Planorbarius corneus* the hermaphrodite duct enters at the junction of the male and female systems, while the albumen gland duct opens into the fertilization pocket and this in turn joins the oviduct (Fig. 8C). As in *Lymnaea*, therefore, the ova do not pass through the albumen gland. The whole of this region is invested in a sheath of muscle fibres and connective tissue.

The albumen gland duct of *Ancylus fluviatilis* similarly opens directly into the fertilization pocket, whilst the hermaphrodite duct, vas deferens and oviduct join on the opposite face of the sac (Fig. 8D).

Thus, it is in the Physidae alone amongst the Hygrophila that the ova pass through the albumen gland and the fertilization pocket is not associated with an albumen gland duct.

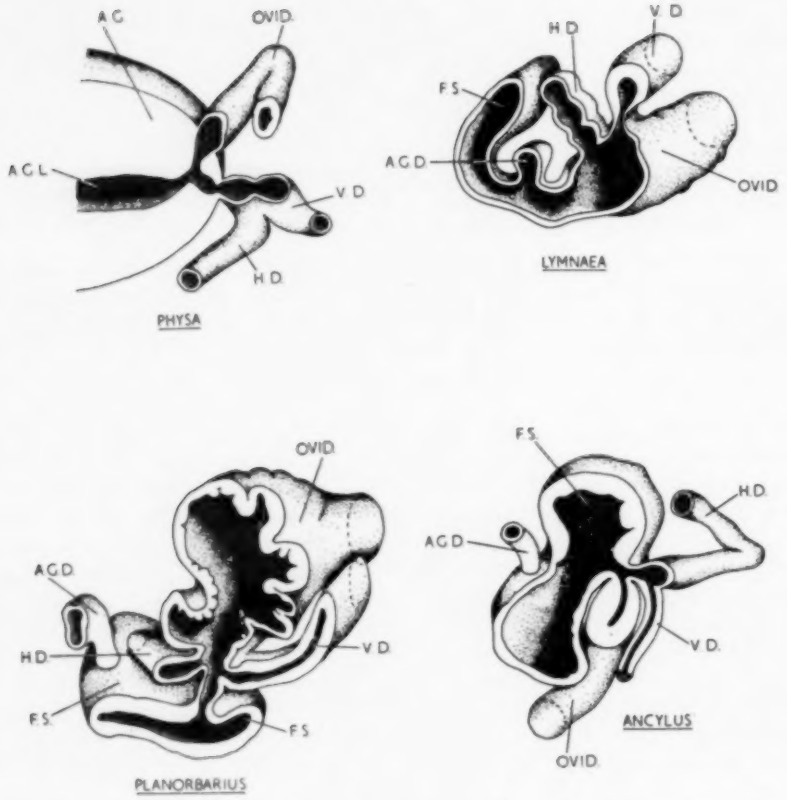

Fig. 8.—Diagrams to illustrate the union of the genital ducts in the region of the fertilization pockets in selected members of the Hygrophila.

(A) *Physa fontinalis*; (B) *Lymnaea peregra*; (C) *Planorbarius corneus*; (D) *Ancylus fluviatilis*.

A.G., albumen gland; A.G.D., albumen gland duct; F.S., fertilization pocket; H.D., hermaphrodite duct; OVID., oviduct; V.D., vas deferens.

The male system

As Hubendick (1947) has pointed out, two fundamentally different types of prostate are found in the Hygrophila. The main secretory elements of the prostate of *Lymnaea peregra* were found to be tall, narrow, columnar cells, packed with granules, whilst in the other three families the prostatic cells are large and cuboidal and differ markedly in histology and staining reaction from those of the Lymnaeidae. In the Physidae the prostatic follicles are developed on the dorsal and lateral walls of the proximal portion of the vas deferens and amongst the Planorbidae a similar arrangement is found in *Gyraulus* spp. (Hubendick & Radoman, 1959) and other genera. In *Planorbarius corneus*, however, the prostate follicles open into a series of

collecting ducts and are contained within a common envelope, so forming a compact organ. There are generally fewer prostate follicles in the Ancylidae, with three in *Ancylus fluviatilis*, but in this species and in *P. corneus* the proximal portion of the vas deferens is composed of columnar, secretory cells whose staining reactions correspond to those of the prostate of these species (see Fig. 7). In the Physidae, however, the vas deferens is formed of a non-glandular, ciliated epithelium (see Duncan, 1958).

The male tract of *Chilina robustior* (a member of one of the more primitive families of the Basommatophora) was found to be lined by prostatic cells similar to those of the *Physa*-type (Duncan, 1960 a). It seems probable that this represents the ancestral condition from which the arrangement in the Physidae, Planorbidae and Ancylidae has arisen by the differentiation of the male duct to form the prostatic follicles, the vas deferens retaining its glandular nature in the last two families. In the structure of the male duct, therefore, the Lymnaeidae differ from the other three families, although, as stated previously (Duncan, 1960 a), the cells of the prostate of *L. peregra* appear to be similar to the prostatic epithelium described in the Ellobiidae (Morton, 1955). In *Ancylus fluviatilis*, the flagellum opens into the penis beside the vas deferens and its histological structure is similar to that of the prostate. The significance of this, however, is not clear although it appears to be an additional secretory organ attached to the male system and has no counterpart in the other families of the Hygrophila.

The female system

In the primitive families of the Basommatophora, the Chilinidae and Ellobiidae, the female tract is simple and in the latter is divided into anterior and posterior mucous glands, whilst in *Chilina robustior* the upper portion of the female system is convoluted and possesses tracts of ciliated cells. Figs. 1A to D illustrate the differentiation of the oviduct found in the Hygrophila and the conditions existing in the Physidae and Lymnaeidae appear to be more primitive ; there is an essential similarity in histology, arrangement and staining reaction to the condition in *Chilina*. An increasing complexity of the egg capsule necessitates a corresponding advance in specialization of the female duct by the formation of additional mucus-secreting areas and glands. The resulting female tract thus appears much more complex than that found in the Chilinidae and Ellobiidae. In all the species studied the epithelium of the oviduct is lined by a basic cell type, a columnar, glandular cell with a mucus-secreting function. The different parts of the oviduct are formed by variations of this basic cell type, by the addition of tracts of ciliated cells and by the development of complex plications, so producing the oothecal glands.

In all four families there is an initial, short conduit which is formed of columnar cells and has a small central lumen. The ducts have a similar structure, are probably homologous and so have been termed oviduct I. Oviduct II is characterized by the presence of bands of ciliated epithelia which are arranged between the tracts of glandular cells. In the Physidae, oviduct II is a diverticulum, whilst in *Lymnaea* it is greatly folded and convoluted and from it opens a blind diverticulum, the muciparous gland, which is regarded

as being part of this region of the oviduct. In *Planorbarius*, oviduct II is a straight tube, but this region is absent in *Ancylus fluviatilis*.

The remainder of the secretory portion of the female system of *Physa*, oviduct III, is a simple sac-like structure, whereas in both *Lymnaea* and *Planorbarius* oviduct II is followed by the oothecal gland. This organ is very similar in the two genera ; the oviduct continues as a ciliated gutter whilst the secretory portion is swollen and folded. This glandular portion is formed of the same cells as are found in oviduct III in *Physa*, and the regions are probably homologous. The condition in *Physa* appears to be primitive, although the oothecal gland is reminiscent of the arrangement in the opisthobranch *Acteon*, where the female duct has a ciliated furrow running along one face (Fretter & Graham, 1954). The ciliated gutter of *Lymnaea* becomes confluent with the cells of the vagina, but in *Planorbarius* the oothecal gland is followed by oviduct IV, which has a characteristic histology. In *Ancylus fluviatilis* the greater part of the female tract consists of a convoluted sac the histology of which is similar to that of the glandular portions of oviduct IV of *Planorbarius* and this term is therefore used. It has an evagination, the ' mucus gland ' which closely resembles it in histological structure and is therefore regarded as belonging to the same region of the female system.

Bondesen (1950) has described the structure of the egg capsules of the Hygrophila. In addition to the vitelline membrane, the eggs are surrounded by tertiary envelopes, these being secreted by the female tract. Initially, each ovum and its galactogen are enclosed in two individual investments, the internal and external membranes. Bondesen regards the unit formed of the ovum, nutritive fluid and internal membrane as the ' egg '. The capsules are completed by the ' eggs ' being enclosed within common investments ; they are embedded in a less gelatinous substance which is bounded by the capsular membrane. Finally, the completed capsule is covered by the slimy pallium gelatinosum. Only, in the Lymnaeidae and Physidae are the ' eggs ' enclosed in an outer, individual envelope, the external membrane. In both *Physa* and *Lymnaea*, oviduct II is greatly developed and it is in this region that the external membrane is secreted (Duncan, 1958 ; Bretschneider, 1948 b). This region of the oviduct is absent in *Ancylus fluviatilis* and exists merely as a straight tube in *Planorbarius* and in these genera the internal membrane only is found (Bondesen, 1950). The viscous fluid in which the ' eggs ' are embedded, together with the capsular membrane, are secreted by the oothecal gland in *Lymnaea stagnalis* (Bretschneider, 1948 b), so that its function is comparable to that of oviduct III in *Physa* (Duncan, 1958). In the Succineidae the ' eggs ' are embedded in a common, gelatinous substance which lacks an outer bounding membrane and this may be related to the relatively simple female tract of *Succinea* (Duncan, 1960).

Thus, to sum up, the Lymnaeidae, with a different prostatic histology, occupy a separate position from the other three families and Hubendick (1947) regards this feature as indicative of a primitive condition. The prostatic epithelium of *Chilina*, however, corresponds with that found in *Physa* and the Lymnaeidae probably represent an early specialization from the ancestral condition. The Planorbidae and Ancylidae both possess a glandular vas

deferens and a further point of similarity is the presence of the apparently specialized histology of oviduct IV. The convoluted oviduct II of *Physa* and *Lymnaea* shows a close resemblance to the posterior portion of the female tract of *Chilina* and if it is assumed that the Chilinidae stand nearest to the ancestors of the Hygrophila, then this suggests that the condition of this part of the female duct in the Physidae and Lymnaeidae is primitive.

It is probable, therefore, that the genital system of the Physidae is nearest to the ancestral condition, while the Planorbidae and Ancylidae have certain features in common and, as Hubendick suggests, represent late offshoots. The genital system of the Lymnaeidae, while retaining several features in common with that of the Physidae, has probably followed a separate evolutionary path.

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SECONDARY EXTERNAL NARES OF THE GANNET

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(With 3 figures in the text)

The gannet has well-developed secondary external nares to compensate for the primary ones which are occluded. It is questionable if this occlusion is a direct consequence of the habit of high diving. Occlusion of the external nares apparently limits the function of the nasal glands as salt excreting organs.

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INTRODUCTION

It is well known that the external nares of the gannet, *Sula bassana*, are occluded and it is usually stated that this is an adaptation related to the bird's habit of diving, head first, into the sea from a considerable height. Less well known are the anatomical adjustments which have been made to replace these essential openings, and which permit the gannet to breathe.

The closure of the external nasal openings in the gannet apparently took place at a remote phylogenetic period. According to Scothorne (1958 and *in litt.*) the embryonic external naris is represented by an osseous lumen which is plugged at the surface with solid epithelium. This plug never breaks down in the gannet as it does in other species during the latter half of incubation, but instead, after hatching, the narrow opening becomes occluded by the overgrowth of bone at its margin.

There is, therefore, in the gannet complete atrophy of an anatomical feature whose functional importance remains undiminished. Obviously, compensation for the lost feature must be made, and this not by any casual and temporary alternative but by a permanent one as efficient as the original both for breathing and for the protection of the nasal passage when the bird is under water. The purpose of this note is to describe such well developed and compensatory secondary nares, and to discuss some points relating to the origin and consequences of this unusual adaptation.

ANATOMICAL FEATURES

The obvious alternative to transnarial breathing is transoral breathing, yet gannets do not display a gaping mouth more frequently than do other

birds. Instead the gannet has developed a permanent gap at the angle of the mouth. This gap is not obvious unless the facial region is viewed from below, because the jugal bar, an element in the formation of the gap, overhangs the lower mandible. This relationship of the jugal bar to the lower mandible (an overlapping without direct contact and with an intermediary slit-like opening) seems to be a characteristic of the architecture of most bird skulls. Usually the angle of the mouth stops short of the jugal bar and therefore no part of the gap is included therein. In the gannet, however, the limit of the mouth has been extended backwards in order to take in as much of the gap as is necessary to form a respiratory opening. This backward extension of the mouth is a characteristic of the gannet's facial expression (Fig. 1).

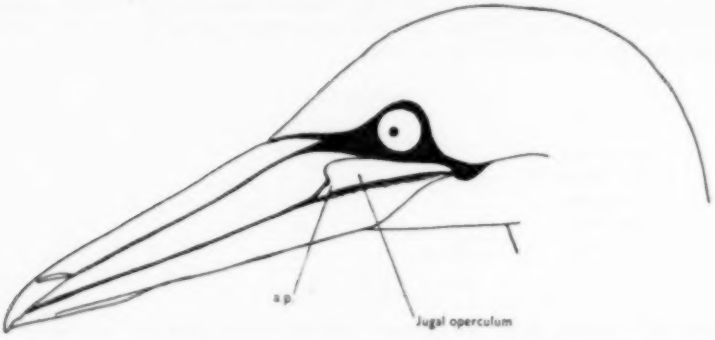

Fig. 1.—Head of gannet, *Sula bassana*, showing position of the 'jugal operculum' covering the secondary external naris. The flexible anterior projection (a.p.) assists in closing the opening on impact with water from a high dive.

The extension of the angle of the mouth for use as a secondary naris also seems to be dependent on certain features which can be used to provide temporary closure of the opening. An important one, already mentioned, is the overlap of jugal bar on lower mandible. In addition, there is slight rotary movement in the jugal bar and also an extension of the cornified epithelium in the jugal region. Movement of the jugal bar is obtained from its flexible connection with the anterior part of the skull (Fig. 2). This flexibility is essential in the many birds, including the gannet, which have a movable upper mandible. The amount of movement in the jugal bar is relatively small and the connection between jugal bar and skull is stronger as a bony, rather than tendinous, joint. The jugo-cranial attachment is a short ligulate piece of bone whose broad axis is horizontal to permit the necessary vertical movement. This connection is sufficiently flexible, in the gannet at least, to allow a small amount of rotary movement also in the jugal bar.

Cornification of the epithelium is a normal feature of the bill. In the gannet the rhamphotheca has been extended backwards to cover the region of the jugal bar. The primary function of this hardening is doubtless protective, as in other parts of the bill, but it has the unusual characteristic, even in species with compound rhamphothecae, of remaining a separate element

and of being connected with adjacent structures by flexible tissues only. It is firmly attached to the jugal bar and, as both have movable connections, this section of the bill can be moved fairly easily by manipulation ; external pressure on it reduces the size of the opening of the secondary external naris (Fig. 3). In life it seems that it is only by the external pressure of water that the opening can be closed. It is difficult to determine the extent of closure when the bird is swimming under water but it seems certain that when it plunges into water from a height the opening is completely shut. An accessory structure which must help to bring this about is a flexible anterior projection to what may be termed the ' jugal operculum '.

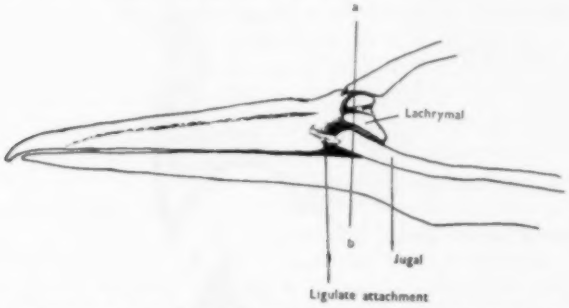

Fig. 2.—Bony features at the angle of the mouth in the gannet showing the flexible ligulate attachment of the jugal bar.

Similar modifications of the angle of the mouth are found in all the gannets and boobies comprising the wide-ranging family Sulidae. It is possible, however, that detailed study might reveal some differences illustrating varying stages in the development of this curious feature. It is beyond the scope of this short notice to discuss what precise adaptations may occur in other birds of habits similar to those of the gannet. Mention will be made only of the fact that a well-developed secondary naris of the gannet type is found in the cormorant, *Phalacrocorax carbo*, and also in some related species, all of which dive under water from surface level. Ewart (1881) and Pycraft (1899) described the main narial features of the cormorant and pointed out that the external nares are open up to a few days before the young bird leaves the nest. It should be noted, however, that the usefulness of the cormorant nares in their functional state must be rather limited since the openings are relatively small. It is the opening in the cormorant rhamphotheca which seals up ; apparently the bony nares never completely ossify, although it is doubtful whether the matter has ever been fully investigated over a wide range of individuals in *P. carbo* or in other members of the Phalacrocoracidae and Anhingidae.

The only other high diver like the gannet is the brown pelican, *Pelicanus occidentalis*, a wide-ranging new world species whose variations include several forms sometimes regarded as species, like the Chilean *thagus*. Alexander (1928) records that brown pelicans ' plunge downwards with such force that the spray dashes high above them, and the resulting splash may be heard half a mile away '. The external nares are not occluded but the apertures

in the rhamphotheca are relatively small and there are flaps of skin so attached that the openings must be closed automatically by water pressure ; also the region of the nasal apertures is streamlined as in the gannet. The external nares seem to be quite inadequate, in relation to the size of the bird, to provide entry of the volume of air necessary for aeration of the pulmonary system.

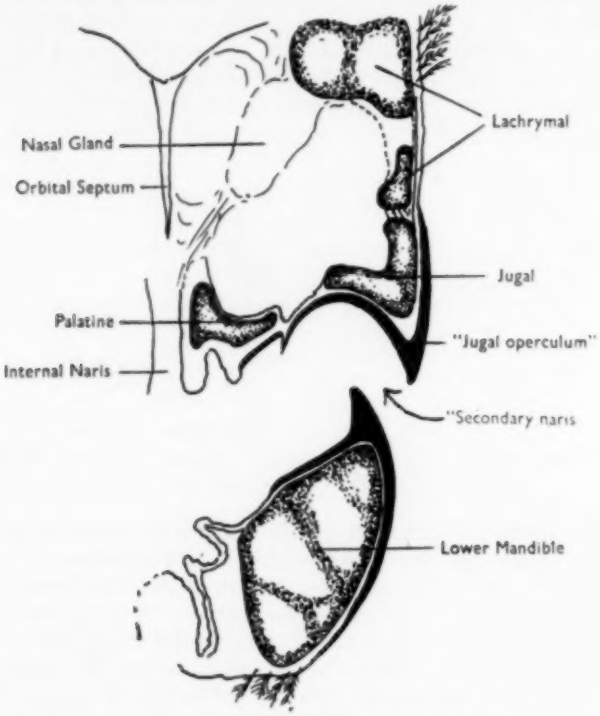

Fig. 3.—Part of the section of a gannet skull, at (a–b) in Fig. 2, showing the gap of the secondary naris when mandibles are otherwise closed. Horny parts are indicated by solid black.

The indication is that the nares in the brown pelican are only partly functional and that they may be evolving towards such complete occlusion as obtains in the gannet.

DISCUSSION

One question which arises from consideration of these anatomical features is the actual relationship between the habit of high diving and occlusion of the external nares. All gannet species manifest a complete narial occlusion at all stages of development and all are high divers ; in cormorant species there is almost complete occlusion in adults although none dives into water from a height ; in the pelicans narial closure is not so advanced as in the cormorants and a cursory examination does not show any lesser degree of closure in those species which are not high divers than obtains in the brown pelican which is. Temporary closure of the external nares, for whatever

necessary reason, seems to be essential in most birds and mammals which normally obtain their livelihood under water. It is possible that permanent closure would follow as a logical development in circumstances where shock damage to the nasal passages (as in violent plunging) would cause injury or death, and when no suitable respiratory alternative was available. By this reasoning the early stage of closure in the pelicans, with only one high diving species, would indicate that as a family they are only in process of acquiring a habit already more or less perfected in the gannets. The situation in cormorants, which is more advanced than in the pelicans, might be explained as one in which the habit of high diving has been lost. But this hypothesis is unsatisfactory. It implies, for example, that some pelicans are evolving occluded nares in anticipation of the need for this feature in relation to the habit of high diving ; so far as is known there is no evidence in any pelican species that the feature is evolving in active response to a habit in course of development. Perhaps the true situation is that occluded external nares have evolved for some other reason. An obvious possibility is that narial occlusion is one form of response to the need for temporary closure in birds which go under water, especially as there is an alternative, and possibly in some respects a better, method of breathing available, as has been demonstrated. But other possible causes should not be lost sight of, for Scothorne states (*in litt.*) that ' narial stenosis is found in some birds which never go under water, let alone dive into it '. The assumption, therefore, that gannets possess occluded external nares because they are high divers is debatable. It is quite possible that this habit of high diving has become practicable because of a narial occlusion evolved in response to some other cause. If this is so then it could be said that cormorants have not yet adapted this anatomical feature to the habit of high diving and that only one pelican species has done so.

To this closure of the external nares in sea birds there is an interesting corollary connected with the function of the nasal glands in excreting sodium chloride when ingested in larger quantities than can be tolerated, as might readily (or of necessity) be the case in birds which feed in salt water and remain for long periods at sea. This nasal gland function was described by Schmidt Nielson *et al.* (1958 a, b, c). All birds associated with salt water, even many coastal species, appear to possess well developed nasal glands (the ' salt glands ' of Schmidt Nielson). Often these glands are so large that they protrude from the nasal socket and excavate great pits in the top of the skull, which pits are a striking feature of most sea bird skulls.

There are, however, no cranial pits in the skull of the brown pelican, nor indeed in the skull of any pelican species. Cranial pits are also lacking in all gannet and cormorant species. The obvious conclusion that nasal (or ' salt ') glands are relatively smaller in these species is confirmed by the rather limited data available on actual gland size. For example, Schmidt Nielson & Fange (1958 a) give the total weight of the nasal gland in the brown pelican as 903 mg (the average of the six figures published) or 300 mg per kilogram of body weight (3·01 kg). Similar estimates in other species are as follows :

Brown Pelican	300 mg/kg	Black-headed Gull	345 mg/kg
Cormorant	140 mg/kg	Common Gull	625 mg/kg
Gannet (a)	105 mg/kg	Herring Gull	1152 mg/kg
(b)	174 mg/kg	Little Auk	1413 mg/kg

These figures are based on gland weights given by Technau (1936) and body weights in the author's personal records. The figure for the little auk is based entirely on a fresh specimen which came to hand in the course of preparing this note. The figure for gannet (b) is based on Technau's gland weight while that for (a) is from glands taken from a fresh specimen, of unknown body weight. The difference in these gannet figures emphasizes the variability in size of the glands in relation to the load of work put upon them ; thus Schmidt Nielson found a ' non-secreting gland to be somewhat smaller in size ', and Schildmacher (1932) found the glands of individual ducks of the same species to be larger when the birds were on salt water than when on fresh. Gannet (a) was taken from the Bass Rock possibly at a time when salt intake was low.

Although it is possible that there may be a fairly wide range of individual variation in nasal gland size it is clear at least that the glands of pelicans, cormorants and gannets are quite appreciably smaller than those of other marine species. Further, it seems that, of the three groups under discussion, the gannet, with the greatest degree of external narial occlusion, has the smallest gland ; the cormorant, with less highly evolved occlusion, has a larger one ; and the pelican, with but partial occlusion, has the largest. The tentative conclusion, therefore, is that the size of the nasal glands, in species in which these glands function as salt-excreting organs, is directly affected by the amount of restriction of the external nares. It is scarcely possible that narial occlusion of itself limits salt intake. Its effect is more likely to be limitation of gland function due to the difficulty of getting rid of the secretory products. These are disposed of through the internal nares and mouth, as was demonstrated in the case of the cormorant by Schmidt Nielson. It may be that marine species with restricted or occluded external nares have found ways of avoiding excessive salt consumption or that their kidneys are specially adapted for a more copious and effective salt excretion.

SUMMARY

(1) Well-developed secondary external nares of the gannet, *Sula bassana*, are described.
(2) The narial features of cormorants and pelicans are referred to.
(3) The relationship between occlusion of the external nares and the habit of high diving is discussed.
(4) Attention is drawn to the apparent reduction in the function of the nasal glands as salt excreting organs in species with occluded and partially occluded nares.

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NOTES ON THE HABITS OF THE TASMANIAN DORMOUSE PHALANGERS *CERCAERTUS NANUS* (DESMAREST) AND *EUDROMICIA LEPIDA* (THOMAS)

BY

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[Accepted 9th February 1960]

(With 1 plate and 4 figures in the text)

The conditions under which specimens of the Tasmanian dormouse phalangers, *Cercaertus nanus* and *Eudromicia lepida*, were found in the field are described. Brief descriptions and measurements of the animals are given.

The activity and dormancy of the two species kept in captivity were investigated daily over a twelve month period. There was no prolonged hibernation. Activity and dormancy alternated throughout the year, the longest period of dormancy in the case of *C. nanus* being twelve days and in the case of *E. lepida* six days.

The body temperature of each species during dormancy was about equal to the air temperature. A dormant specimen of *C. nanus* having a body temperature of 12·5°C. took three hours to become fully active, when roused from dormancy. During this period the body temperature rose to 31°C. In the same way a dormant specimen of *E. lepida* having a body temperature of 17°C. required three hours and forty minutes to become fully active, its body temperature rising to 32°C.

The food and feeding habits of both species were studied, and found to be much the same. Insects were preferred but spiders, dead scorpions and even lizards were readily accepted. The flowers of *Eucalyptus* and *Banksia* were pulled to pieces but not eaten.

During periods of activity the daily food consumption amounted to about seven per cent of the body-weight of the animal in each case.

The composition of an artificial food on which the animals thrived is given.

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INTRODUCTION

The dormouse phalangers, known also as pygmy opossums or opossum mice, are represented in Tasmania by two species, namely *Cercaertus nanus* (=*Dromicia nana* (Desmarest)) and *Eudromicia lepida* (Thomas). The former occurs also on the mainland of Australia, but the latter has been recorded only from Tasmania. Although both species live readily in captivity and are sometimes kept as pets, little appears to have been written concerning their habits, especially their dormancy and so-called hibernation. Brief

observations on the habits of *C. nanus* have been recorded by Gould (1845), Le Souef & Burrell (1926), Chaffer (1930) and Troughton (1931). Statements concerning the hibernation of the animal are often conflicting and lack confirmation. Thus Le Souef & Burrell (1926) claim that in winter dormouse phalangers go into complete hibernation. Miss S. D. Bocking, quoted by Troughton (1943), remarks that *C. nanus* appears to undergo a semi-hibernation twice yearly. Eisentraut (1953) mentions that *C. nanus* is the only marsupial, in which 'Winterschlaf' has been observed with certainty. Krumbiegel (1955) states, '*Dromicia* ist Trockenschläfer'.

In regard to the habits of *Eudromicia lepida* even less appears to be known than in the case of *C. nanus*. Lord & Scott (1924) claim that the two species have much the same habits, but give little information to substantiate the statement.

The notes presented in the following pages are based mainly on daily observations of two females of *C. nanus* and two females of *E. lepida* kept in captivity. The observations cover a period of thirty months in the case of both specimens of *C. nanus* and forty-two months in the case of one specimen of *E. lepida*, twenty-two months in the case of the other.

METHODS

The animals were housed in separate observation cages, which at first were kept indoors but later transferred to a garden, where they remained for over twelve months. The cages used for *C. nanus* measured 62·0 cm. high, 47·0 cm. wide and 21·0 cm. deep. Each was furnished with a removable sleeping box in an upper corner at the back of the cage. The sleeping box was 18·0 cm. long, 14·0 cm. wide and 13·0 cm. high. At one end it was provided with an entrance hole 4·0 cm. in diameter. Strands of bark, moss and cotton wool were placed in the boxes to serve as nesting materials. Small branches from a tree were fixed in the cages enabling the animals to climb up to and down from the sleeping boxes.

The cages and sleeping boxes provided for *E. lepida* were similar to those for *C. nanus*, but slightly smaller.

When necessary, body temperatures were taken with a short-stem thermometer placed in such a position that the body of the animal was curled round the bulb of the instrument. No attempt was made to take rectal temperatures.

FIELD NOTES AND MEASUREMENTS

The two specimens of *C. nanus* were found in an area of small dead eucalypts on the slopes of Mount Wellington at an altitude of about 3300 feet. The first one was discovered on 4th April, 1957, and the second a week later. Each was in a state of dormancy and occupied a small cavity in the stump of a dead tree. The stump in which the first specimen was found measured about 183·0 cm. high and 55·0 cm. in diameter. On the outside it was firm and solid, but in the centre decayed and crumbling. In the central mass of decayed wood the animal had made a vertical burrow, 3·5 cm. in diameter and extending downwards to a depth of 9·0 cm. The lower end of the burrow

opened into a small cavity, 6·5 cm. in diameter, within which the phalanger was lying in a curled up position (Pl. 1, fig. a). The cavity contained no nesting materials, such as leaves or bark, and was merely an excavation in the decaying wood. The entrance to the vertical burrow was closed with loosely packed particles of rotten wood.

The animal was removed and allowed to awaken from its dormancy. On being returned to the cavity in the stump, it immediately commenced to burrow more deeply, using its fore-paws to scratch out the crumbling wood.

The second specimen was found in a similar stump, the centre of which consisted of soft decaying wood into which the phalanger had burrowed. However, the cavity occupied by the animal was situated at a much greater depth from the surface, the vertical tunnel being 61·0 cm. in length. As in the previous case the entrance was closed with loosely packed particles of crumbling wood and no nesting materials were present in the terminal chamber.

The two specimens of *E. lepida* were found near a creek in a heavily timbered valley at the foot of Mount Wellington. The first specimen, a fully grown female, was taken on 28th April, 1956. It was dormant and curled up in a small cavity in the broken end of an exposed root of a fallen tree. The end of the root was horizontal and about 90·0 cm. above the ground. The cavity occupied by the phalanger was in moderately hard wood and could not have been excavated by the animal. No nest had been constructed, but the cavity was overgrown with moss and thus effectively concealed.

The second specimen of *E. lepida* was found on 12th December, 1957. It was an immature female little more than half grown. The animal was dormant and curled up in a small dome-shaped nest of bark fibres. The nest was situated about 35·0 cm. inside a broken hollow branch of a fallen tree. The branch was horizontal and about 135·0 cm. above the ground. It was located in deep shade.

The two specimens of *C. nanus* were of the usual dull grey colour above with the underparts and feet almost white. The eyes were large and prominent, each being surrounded by a dark area (Pl. 1, fig. b). The base of the prehensile tail had the characteristic incrassate form.

The two examples of *E. lepida* were brownish grey above, the underparts and feet being white with a fawnish tinge. The eyes were not as prominent as in the preceding species, nor were the dark areas surrounding them so strongly marked. The base of the tail was thickened as in *C. nanus* (Pl. 1, fig. d).

The four animals have thrived in captivity and the immature specimen of *E. lepida* is now fully grown. Measurements of the four specimens are given in Table 1.

ACTIVITY AND DORMANCY

It is generally claimed that the dormouse phalangers are strictly nocturnal in habit. This, however, was not the case with the specimens of *C. nanus* and *E. lepida* studied in the present investigation. Although they generally remained in their sleeping boxes until dusk before coming out to feed, there

TABLE 1

Length measurements of *Cercaertus nanus* and *Eudromicia lepida* in mm.

	Cercaertus nanus		*Eudromicia lepida*	
	Specimen 1	Specimen 2	Specimen 1	Specimen 2
Head and body	98·0	100·0	70·0	70·0
Tail	95·0	87·0	78·0	63·0
Hind foot	16·0	16·0	13·0	13·0
Ear	16·0	17·0	15·0	15·0

were occasions when they came out even at midday or in the afternoon, especially if the sky were clouded and the light dull.

Daily observations made over a twelve months period from 1st October, 1958, to 30th September, 1959, showed that for each species periods of activity alternated with periods of dormancy throughout the year and that no prolonged hibernation occurred. The periods of activity tended to be longer and those of dormancy shorter during the six months September to February, whilst the reverse was the case during March to August (Figs. 1 and 2).

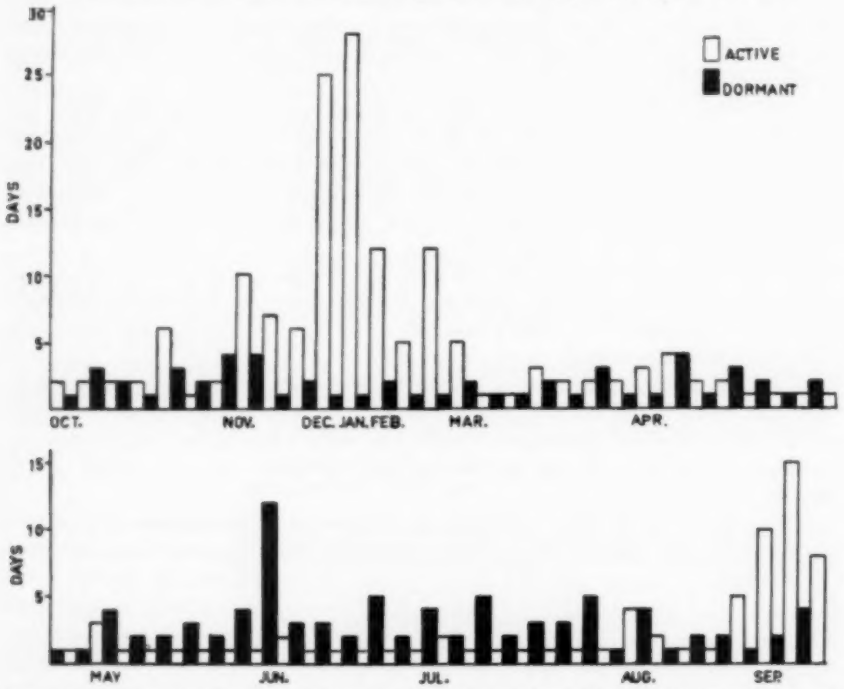

Fig. 1.—Diagram showing the duration in days of the alternating periods of activity and dormancy exhibited by *Cercaertus nanus* in the twelve months from 1st October, 1958, to 30th September, 1959.

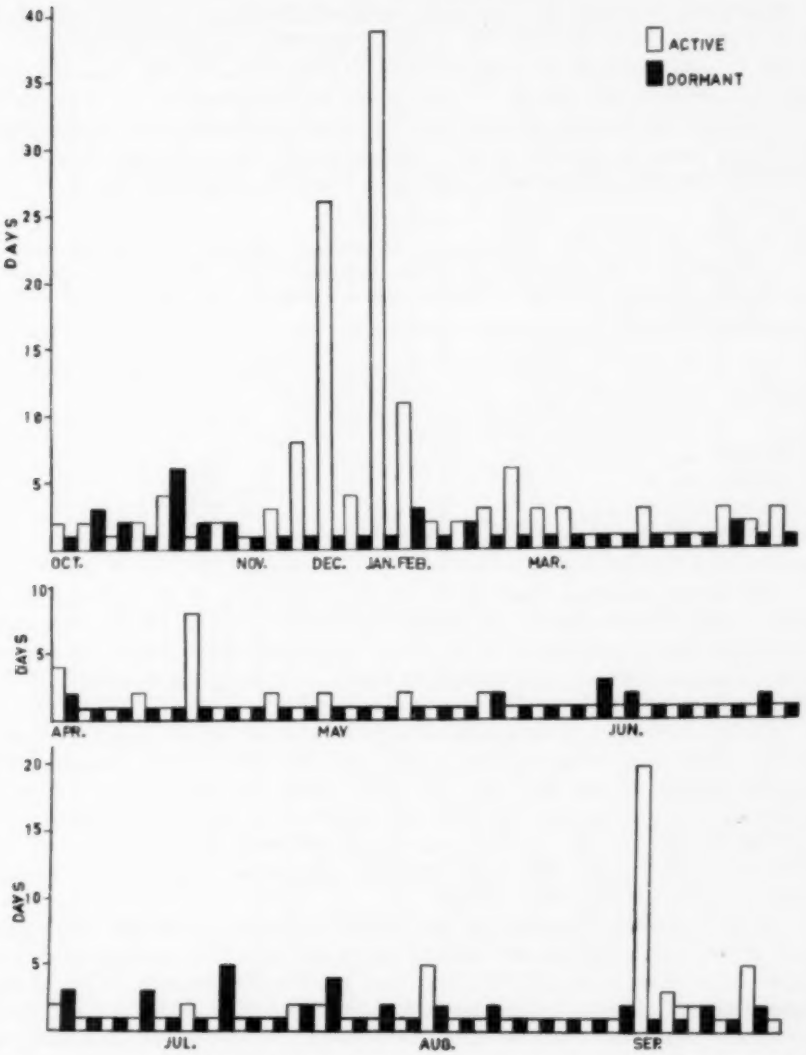

Fig. 2.—Diagram showing the duration in days of the alternating periods of activity and dormancy exhibited by *Eudromicia lepida* in the twelve months from 1st October, 1958, to 30th September, 1959.

In each species individual differences both in the total number of days of activity and in the maximum duration of a period of activity were exhibited. However, individual differences in the maximum duration of a period of dormancy were slight or absent (Table 2). In the case of *C. nanus* the maximum period of dormancy was about twice that of *E. lepida*.

The air temperature in the vicinity of the observation cages was recorded each night at about 10 p.m. It varied during the twelve months from 2° C. to 28° C. and there did not appear to be any direct correlation between the temperature and the activity or dormancy of the animals. On two days when the temperature had fallen to 2° C., both specimens of *C. nanus* were active on one day and dormant on the other. At temperatures from 2° C. to 18° C. the two animals were sometimes dormant, sometimes active.

TABLE 2

Total number of days of activity and of dormancy and also the maximum duration of a period of activity and a period of dormancy exhibited by the specimens of *Cercaertus nanus* and *Eudromicia lepida* during the twelve months from 1st October, 1958, to 30th September, 1959.

	Total number of days of		Maximum duration of a period of	
	Activity	Dormancy	Activity	Dormancy
C. nanus (No. 1)	224	141	28	12
C. nanus (No. 2)	284	81	99	10
E. lepida (No. 1)	245	120	39	6
E. lepida (No. 2)	258	107	79	6

On the five occasions when the temperature was below 4° C. both specimens of *E. lepida* were dormant. At temperatures from 4° C. to 19° C. in the case of one specimen, and from 4° C. to 15° C. in the case of the other, the animal was sometimes dormant and sometimes active. At temperatures above 19° C. the specimens of both species were active (Table 3).

During dormancy *C. nanus* and *E. lepida* adopted similar positions of the body. They both curled up into a ball with the muzzle resting against the ventral surface of the abdomen, the eyes closed, the ears folded and bent downwards at the sides of the head, the digits of manus and pes flexed, and the tail coiled in a flat spiral at one side of the body (Pl. 1, fig. c). If the dormant animal were disturbed, it would sometimes make a faint hissing noise without altering its position.

In both species regulation of the body temperature appeared very weak and the dormant animal felt cold to the hand. Its body temperature was equal to or sometimes slightly less than the air temperature. One of the specimens of *C. nanus*, which was dormant on 28th May, 1958, and had been so for five days, was removed from its sleeping box and placed on a table at 1.15 p.m. Its body temperature was then 12·5° C. and equal to the air temperature. During the next three hours the phalanger gradually awoke from dormancy. The body temperature was taken at intervals throughout the waking period. In the first ninety minutes it rose gradually to 20° C. and in the next ten minutes it increased sharply to 27° C. (Fig. 3). At this stage the animal raised its head slightly and opened its eyes. At 4.15 p.m. the body temperature had risen to 31° C. and the animal had become fully active. During the three hours the air temperature had remained constant at 12·5° C.

TABLE 3

Number of days the specimens of *Cercaertus nanus* and *Eudromicia lepida* were active or dormant in relation to the nocturnal air temperatures during the twelve months from 1st October, 1958, to 30th September, 1959.

Air Temp. °C	*Cercaertus nanus*				*Eudromicia lepida*			
	Specimen No. 1		Specimen No. 2		Specimen No. 1		Specimen No. 2	
	Active	Dormant	Active	Dormant	Active	Dormant	Active	Dormant
2	1	1	1	1	–	2	–	2
3	1	2	1	2	–	3	–	3
4	1	7	3	5	3	5	3	5
5	6	4	5	5	6	4	5	5
6	7	10	7	10	5	12	4	13
7	2	12	6	8	7	7	7	7
8	13	17	17	13	13	17	10	20
9	13	15	15	13	12	16	10	18
10	15	15	25	5	22	8	21	9
11	22	19	33	8	29	12	27	14
12	18	9	23	4	21	6	22	5
13	16	13	27	2	19	10	26	3
14	26	8	32	2	25	9	32	2
15	13	5	17	1	15	3	17	1
16	16	1	17	–	15	2	17	–
17	17	2	18	1	18	1	19	–
18	16	1	16	1	15	2	17	–
19	10	–	10	–	9	1	10	–
20	2	–	2	–	2	–	2	–
21	3	–	3	–	3	–	3	–
22	2	–	2	–	2	–	2	–
23	1	–	1	–	1	–	1	–
24	1	–	1	–	1	–	1	–
25	1	–	1	–	1	–	1	–
28	1	–	1	–	1	–	1	–
Totals	224	141	284	81	245	120	258	107

Unavoidable disturbance of the animal made it difficult to measure accurately the rate at which the body temperature fell, when the phalanger passed from a fully active condition to one of dormancy. However, it was observed in the case of the second specimen of *C. nanus* that the body temperature fell eighteen degrees in less than twelve hours. At 9.15 p.m. on 2nd June, 1958, the animal was fully active and had a body temperature of 33° C. On the following morning at 9.15 a.m. it was dormant and its body temperature 15° C. The air temperature over the same period rose two degrees, that is from 14° C. to 16° C.

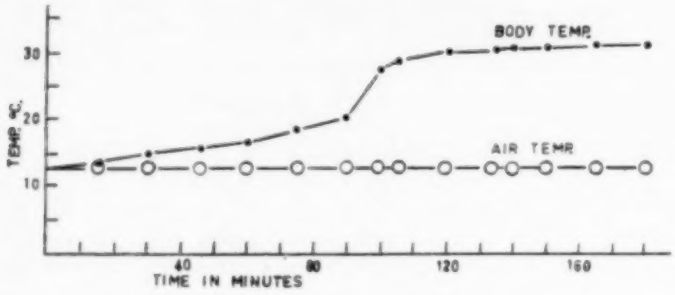

Fig. 3.—Graph showing the rise in body temperature of *Cercaertus nanus* as the animal awakes from dormancy.

When *E. lepida* awakes from dormancy its body temperature rises in much the same way as in the preceding species. Thus a specimen, which was dormant at 10 a.m. on 4th June, 1958, had a body temperature of 15° C., which was equal to the air temperature. During the next four and a half hours the animal was left undisturbed in its sleeping box and its body temperature rose with the air temperature to 17° C. It was then removed from the sleeping box and placed on a table. Here it remained curled up in a dormant position for two hours, during which time its body temperature and the air temperature remained constant at 17° C. Between 4.30 p.m. and 5 p.m. the body temperature rose from 17° C. to 27° C., but the animal did not become fully active until 6.10 p.m., when its body temperature had risen to 32° C. The air temperature remained near 17° C. during the waking period (Fig. 4).

FOOD AND FEEDING HABITS

Some information on the food of *C. nanus* has already been given by Gould (1845), Lucas & Le Souef (1909), Le Souef & Burrell (1926), and Troughton (1931).

Our Tasmanian specimens of *C. nanus* exhibited a marked preference for insects. Cicadas, the common mantis (*Orthodera ministralis*), termites (*Porotermes adamsoni*) and both larvae and adults of various Coleoptera, especially those belonging to the families Elateridae, Scarabaeidae and Cerambycidae, were all readily accepted. When the insect was not too large it was held in the fore-paws while being eaten (Pl. 1, fig. b). A large longicorn

larva was always turned round so that the end of its abdomen could be bitten off. The intestine was then seized between the front teeth, pulled out and rejected. The other internal organs of the larva were eaten, the chitinous exoskeleton being left over.

A moth placed in the cage would sometimes be caught while in flight, the phalanger seizing it with its fore-paws. The wings were then bitten off and rejected, the rest of the body being eaten. Many different moths were accepted, but the common tiger-moth, *Ardices glatignyi*, was always refused. The mere fluttering of a moth in the entrance to the cage was often sufficient to attract the phalanger out of its sleeping box.

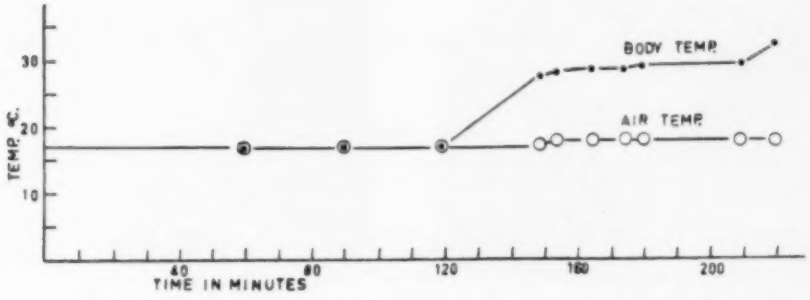

Fig. 4.—Graph showing the rise in body temperature of *Eudromicia lepida* as the animal awakes from dormancy.

The scorpion (*Cercophonius squama*) and the large spider (*Delena cancerides*), if previously killed, were also readily taken as food.

Lizards (*Lygosoma metallicum* and *Lygosoma trilineatum*) up to about 10 cm in length were quickly caught and eaten alive from the tail end forward. One one occasion *C. nanus* was observed to employ one of its hind feet to hold down the struggling body of a small lizard, while it seized the detached and wriggling tail with its fore-paws. With the exception of the scales and claws the whole body of the lizard was devoured.

It has been claimed by some authorities that *C. nanus* is also phytophagous and that it will eat *Eucalyptus* and *Banksia* flowers. However, our Tasmanian specimens, when offered such flowers, merely pulled them to pieces, as if searching for insects or nectar. They did not appear to eat them.

An artificial food on which the animals thrived consisted of lightly baked biscuits made from a mixture consisting of self-raising flour (350 grm.), corn-flour (70 grm.), cane sugar (220 grm.), butter (110 grm.), salt (1·5 grm.), milk (20 ml.) and one egg.

Each day during periods of activity *C. nanus* ate an amount of food equal to about seven per cent of its own weight. Thus for example a specimen weighing 59·3 grm. consumed on four consecutive days 4·0, 4·5, 4·4 and 3·8 grm. respectively.

After feeding on moist food the phalanger frequently rubbed its fore-paws together and then licked them in order to clean them. It would then rub its muzzle with its paws.

In drinking *C. nanus* lapped up water with its tongue in much the same way as a cat drinks. During periods of activity in summer the daily intake of water was about 4 ml.

The two specimens of *E. lepida* showed a preference for the same foods as those accepted by *C. nanus*. They readily fed on insects, spiders and small lizards. The flowers of *Banksia* and *Eucalyptus* were pulled to pieces but not eaten. The weight of food consumed each day during periods of activity was about 6·8 per cent of the body weight of the animal. Thus for example a specimen weighing 15·7 grm. ate on four consecutive days 1·53, 0·52, 1·06 and 1·16 grm. respectively.

In its mode of drinking and in the way it cleaned its fore-paws and muzzle *E. lepida* resembled *C. nanus*.

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a. *Cercaertus nanus* in end chamber of burrow in the decayed wood of a dead eucalypt stump.

b. *Cercaertus nanus* feeding on a longicorn larva held in the left fore-paw.

c. *Eudromicia lepida* when dormant.

d. *Eudromicia lepida* when active.

OBSERVATIONS ON THE SEALS OF THE (WELSH) DEE ESTUARY

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(With 2 plates and 5 figures in the text)

The existence of a large non-breeding gathering of seals in the (Welsh) Dee has been established. Detailed counts for a period of several years are given and certain characteristics of the gathering are described.

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INTRODUCTION

The following observations were made on a colony of seals seen, according to the state of the tide, in the waters and on the sandbanks around the Hilbre group of islands situated in the mouth of the (Welsh) Dee estuary. Craggs has observed them weekly—with a few exceptions—for the past six years ; Ellison at less regular intervals over a longer period. Practically all are referable to the grey seal *Halichoerus grypus* (Fabricus), but there is evidence that the common seal *Phoca vitulina* L. also occurs there.

Coward (1910) described the status of the seals in the estuaries of the Mersey and Dee as :

Grey seal " Has occurred occasionally ".

Common seal " An occasional wanderer to the estuaries ".

This may have been reasonably accurate up to about 1939, as no larger number than three seals together are recorded in the Annual Reports of the Lancashire and Cheshire Fauna Committee ; but we learn from local fishermen that a herd of a dozen or so might be seen occasionally on the West Hoyle Bank, during the early thirties.

SITE

The Hilbre group are islands only at high tide ; at other times they are joined to the mainland more than a mile distant, by a flat expanse of wet sand (Fig. 1). A deep water channel, Hilbre Swash, runs parallel to the islands on their west side and separates them from the West Hoyle Bank. This sandbank dries out completely between approximately half-ebb and half-flood when an

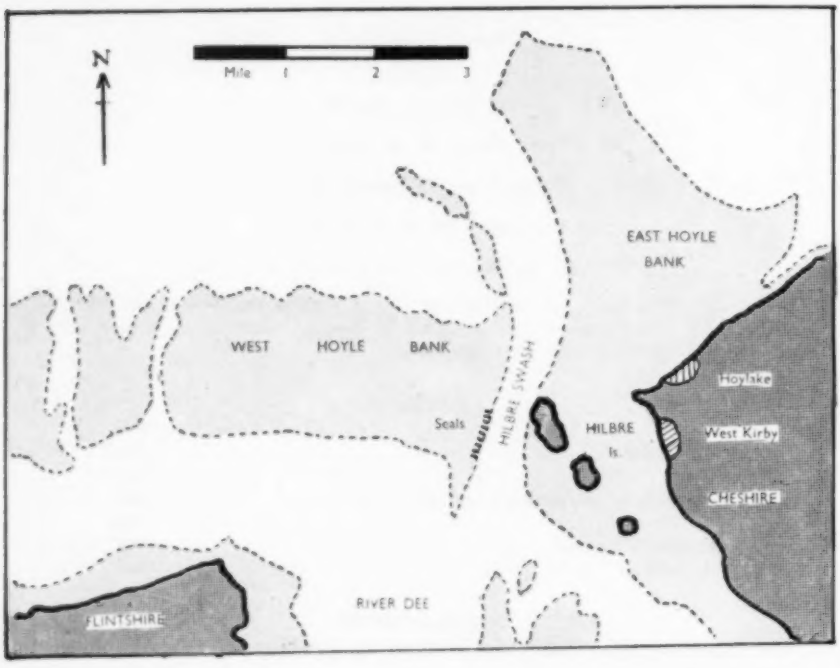


Fig. 1.—Map of Hilbre Island and the West Hoyle Bank. Cross-hatching—above high water mark ; dotted—between low and high water marks.

area of about fourteen square miles of fine sand with no traces of stones or mud is exposed. The seals haul out on this bank about half-way along its eastern side, always choosing approximately the same place for a reason not apparent to us. Hauling out sites of this kind (sandbanks) for non-breeding assemblies of grey seals are extremely rare. The distance from Hilbre to the nearest known breeding grounds (Puffin Island) is about thirty-three miles. The Puffin Island colony is very small and the distance to the large colonies, e.g. Ramsey Island, is much greater.

METHODS OF IDENTIFICATION AND COUNTING

Many of our observations have been made from the top of the 60 foot cliff on Hilbre, through binoculars or a powerful telescope across a distance of

about half-a-mile. Two factors have prevented closer inspection ; the shyness of the seals themselves, and the great difficulty of hiring a boat locally. The seals bunch together three or four deep and so a definite count is not always possible, but we think our figures are accurate within 5 per cent. Only those seals hauled out or half-submerged at the edge are included ; those swimming further out in the Swash with only the head visible are not.

Identification has been by sight only, i.e. by comparison in size and by the shape of the head in profile. Approaching full tide, a few seals are usually seen near to Hilbre when it is possible to examine them at a distance of 50–100 yards or even less. We have watched the seals in this way many times, and all we have seen in these circumstances have been grey seals. Both of us are familiar with the common seal elsewhere. Only two dead specimens have been washed ashore (on 15 : 8 : 1951 and in November 1957) in the past ten years and both were adult bull grey seals, length *ca.* 7 feet and 7 feet 1 inch respectively. Another specimen, taken alive at New Brighton some five miles along the coast, and afterwards released by Ellison at West Kirby on 17 : 1 : 1955, was also a grey seal, length *ca.* 40 inches. It was too fierce to allow any examination of the teeth or sex, but it was almost certainly a young female. On three occasions it has been possible to approach by boat to within 200 yards of the colony. On 29 : 9 : 1955 Mr W. Wilson, in a canoe, noted that all on the Bank were grey seals. On 18 : 7 : 1956 we managed to get within 150 yards of some thirty seals hauled out on the Bank and found all were grey seals. We noted among them the largest bull we have yet seen and estimated his length to be nearly 8 feet.

Mr R. K. Perry, Keeper of the Department of Vertebrate Zoology, Liverpool Museums, has published in the Annual Reports of the Lancashire and Cheshire Fauna Committee three records of the common seal *Phoca vitulina* L. for the period August 1930 to September 1932.

Mr Perry also records three adult common seals frequenting the Swash and hauling out during December 1933. Later he notes that " both Grey and Common Seals have been observed off Hilbre during October, November and December 1934 ". Subsequently in 1945 and 1946, herds of eighteen, thirty-two and thirty-three seals on the Bank were recorded as common seals, but in view of our investigations since then, we consider these identifications to be doubtful. There is the possibility that the great increase in the number of grey seals has driven away the common seals, but we have no evidence to support this.

On 18 : 12 : 1952 an adult common seal came ashore alive at West Kirby, length 35½ in. Professor Hewer confirmed the identification from photographs.

The following counts of seals hauled out on the West Hoyle Bank show how the colony has increased :

Aug. 1942	*Aug.* '45	*July* '50	*Aug.* '52	*Dec.* '54	*July* '56	*Feb.* '57
14	32	50 plus	80	94	111 plus	117

The reasons for this rapid increase here, or the colonies whence these seals have come, are not known.

We have made many sight records of the seals over the last five or six years and the results of careful counts made on these occasions are plotted

in Fig. 2. Where possible, visual counts were supplemented by photographic records, although the number of the latter are necessarily small. We have been careful to under-estimate the counts as on many occasions the seals are closely packed together ; indeed there have been times when, for this reason, we have been unable to take counts at all. This packing is clearly shown on Plate 1, fig. 1.

The appearance of the hauled out groups is shown in our photographs (Plate 1, figs. 1 and 2 ; Plate 2, fig. 3). These are representative of a large number taken with a camera specially built at the University of Liverpool. This camera was constructed round an aerial survey 36 in. F 6·3 lens which was specially tested for resolution. The excellent performance of this lens may be judged from the fact that it is possible to resolve the legs of a herring gull at a range of *ca.* 1,000 yards. Very often this perfection could not be obtained because of high winds or adverse atmospheric conditions, such as shimmering. Where possible, photographs were taken when some of the seals presented themselves in profile and from these photographs we feel confident that they show grey seals. Photographs taken on 1st October 1956 by Mr Eric Hosking from a boat at comparatively close range, and now reproduced in Plate 2, figs. 4 and 5, confirm our identification as grey seals.

Our observations show that usually there is a preponderance of brown or light grey seals in the group. Frequently we have noticed apparently pure white individuals. These were of such a size and were seen at such times of the year that they cannot have been pups. The number of apparently mature males, judged by size and colour, was always small.

We have noted that if the prevailing wind comes strongly from any point between east and north the seals do not usually haul out, and we do not think that either the temperature or the force of the wind are the reasons for this. A much stronger, and equally cold, wind from the north-west does not keep them in the water. The curvature of the Bank is hardly sufficient to provide a lee when they haul ashore on its eastern edge. Indeed, in a strong north-west wind we have often seen them partly covered by drift sand blown off the top of the Bank. Heavy rain is ignored even when they are hauled out.

We had a good example of this reaction to an easterly wind on 18 : 7 : 1956. The wind had been light, easterly and not cold before we set off in a motor-boat. Although it was past half-ebb not a seal was visible on the Bank and we debated whether to continue or not. Half-an-hour later, as we approached the Bank, the wind backed suddenly to the north-west and within the next twenty minutes more than thirty seals had hauled out. The Swash evidently was full of small, silvery fish which kept leaping out of the water in three's and four's before the onslaughts of the several seals still fishing.

At low tide a number of herring gulls, *Larus argentatus* Pont. and lesser black-backed gulls, *Larus fuscus* L. are scattered over the Bank, but there is always a noticeable concentration around the hauled out seals. We have never seen the gulls pick up any food there and cannot understand why they seek the company of the seals. In observations on a colony of common seals, Venables & Venables (1955) have noted a similar occurrence.

SEAL COUNTS

The counts shown in Fig. 2 provide evidence of two seasonal peaks, in and about June–July, and December–January. There seems to be a marked reduction in numbers in October. We do not offer any interpretation of these observations but it is tempting to attempt to relate them in some way with the breeding season of the Ramsey seals (usually September to November).

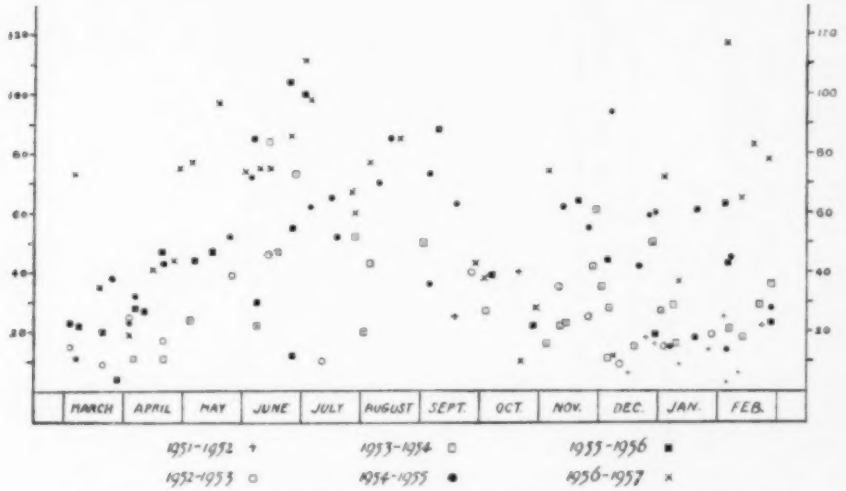


Fig. 2.—Distribution of grey seal counts from September 1951 to February 1957.

Thus the autumn peak, which observations show to be composed mainly of immature seals, may be linked with the simultaneous concentration of breeding seals on Ramsey. The summer peak also needs an explanation of course and there again the majority of seals appear to be immature. We are basing the latter suggestion on data (colour, size, etc.) published by Davies (1949).

The day-to-day fluctuations in the size of the hauled out groups are large (Fig. 2). Professor Pumphrey suggested to us that these fluctuations might be due to the inclusion of counts taken with unfavourable winds (E to NE to N) (see the above account of this phenomenon) but a re-examination of the data showed that such counts are too infrequent to have any appreciable effect. The fluctuations may well be connected with temporal variations in the local food supply.

The counts exhibited graphically in Fig. 2 are reproduced in tabular form (see Table 1). Here individual counts are given for each month for each of the six years during which observations were made. In columns 8 and 9 respectively, the average count per month and the highest count in each month are given. We think it worth while to give these data in full so that further analysis of them can be made.

TABLE 1

Population counts in detail.

	1951–52	1952–53	1953–54	1954–55	1955–56	1956–57	No. of observations	Average count per month	Highest count in each month
March		15		11	23	73	10	26	73
		9		38	22	35			
					20				
					4				
April		25	11	23	28	75	14	32	75
		17	11	32	27	19			
				43	47	41			
						44			
May		39	24	52	44	77	7	55	97
					47	97			
June		46	22	72	85	74	15	62	104
		47	84		30	75			
			73		104	75			
					55	86			
					12				
July		10	52	62	100	98	10	68	111
				65		60			
				52		111			
						67			
August			20	70		77	6	63	85
			43	85		85			

				36					
				63					
October	40		27		39	38	7	28	40
					22	10			
						28			
November		35	16	62	64	74	11	44	74
		25	22	55					
			23						
			42						
			62						
December	6	9	35	94	44		16	32	94
	18		28	42	12				
	16		11	59	19				
			15	60					
			50						
January	9	15	27	15	61	72	12	28	72
	14	19	29	18		37			
			16						
February	25		21	14	63	65	18	40	117
	3		18	45	43	83			
	6		29	28	23	78			
	22		36			117			
Observations per year	11	14	28	26	26	29		TOTAL 134	
Highest count in each year	40	47	84	94	104	117			

In Table 2 for convenience, are shown monthly analyses for each year, and in column 7, the average of all the monthly averages taken over the whole period, again for each month. In column 8 we have included data on the Farne Islands colony, from a publication by Mrs Hickling (1957).

TABLE 2

Monthly averages of counts for each year. Nos. of counts are given in brackets.

	1951–52	1952–53	1953–54	1954–55	1955–56	1956–57	Monthly Averages for the 6 years	Monthly Averages 1956–57 Farne Islands
March		12(2)		25(2)	17(4)	54(2)	26	1152(1)
April		21(2)	11(2)	33(3)	17(3)	45(4)	32	793(3)
May		39(1)	24(1)	52(1)	45(2)	87(2)	55	
June		46(2)	66(3)	72(1)	57(5)	77(4)	62	132(1)
July		10(1)	52(1)	60(3)	109(1)	84(4)	68	380(1)
August			32(2)	77(2)		81(2)	63	385(1)
September	25(1)	40(1)	50(1)	61(3)	78(1)	43(1)	51	730(3)
October	40(1)		27(1)		30(2)	25(3)	28	790(3)
November		30(2)	35(5)	58(2)	64(1)	74(1)	44	487(1)
December	13(3)	9(1)	28(5)	64(4)	25(3)		32	571(1)
January	12(2)	17(2)	24(3)	16(2)	61(1)	54(2)	28	1185(1)
February	14(4)		26(4)	29(3)	43(3)	86(4)	40	1006(2)

We are especially indebted to Professor Hewer for suggesting ways in which the counts can be represented as shown in Figs. 3, 4 and 5. Figure 3 shows the maximum and average counts for each month taken over the six-year period. It shows clearly, from the maximum counts, the two peaks in the population cycle ; namely in or about June–July and December–February. It will be noted that these two periods are about six months apart. It is also apparent from Fig. 3 that the monthly averages for the summer period reflect the population peak, but the winter monthly averages do not show this peak so clearly. This may be due either to the effect of changeable weather or to a change in behaviour of the seals from summer to winter.

Since the peak of breeding of the Welsh (mainly the Ramsey colony) and Irish seals seems to be at about the end of September, it would be expected that in October the maximum number of adults would be on the breeding grounds, which agrees with our period of minimum population. By November the adults and juveniles would have left the breeding grounds to increase the populations at non-breeding stations, such as Hilbre. These points could presumably be checked by observations on the age distributions in the Hilbre colony through the year, but this would be a difficult operation which may perhaps be undertaken in the future.

Figure 4 gives a simple plot of the maximum count in each year as a function of time. Despite the inherent inaccuracies in the counting, we feel that the number of counts made over the six-year period makes it reasonably certain

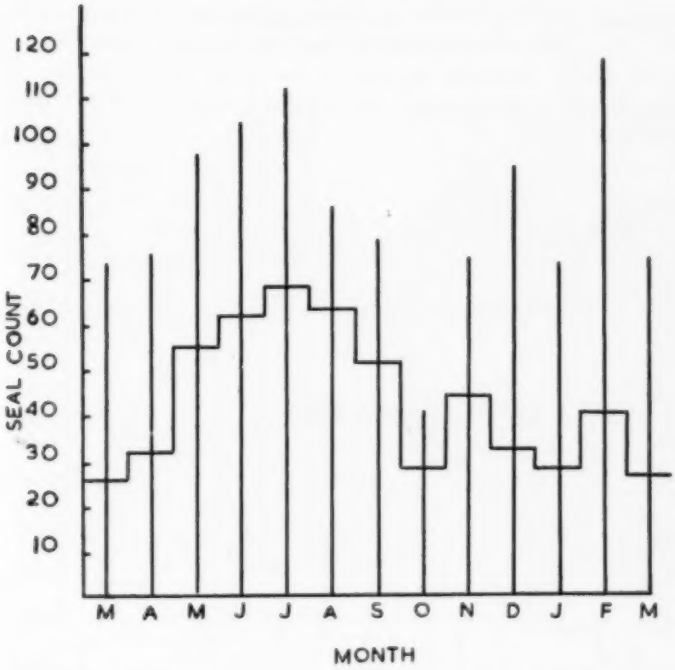


Fig. 3.—Seal counts, 1951–1957 ; histogram—average monthly values ; vertical lines—maximum monthly counts.

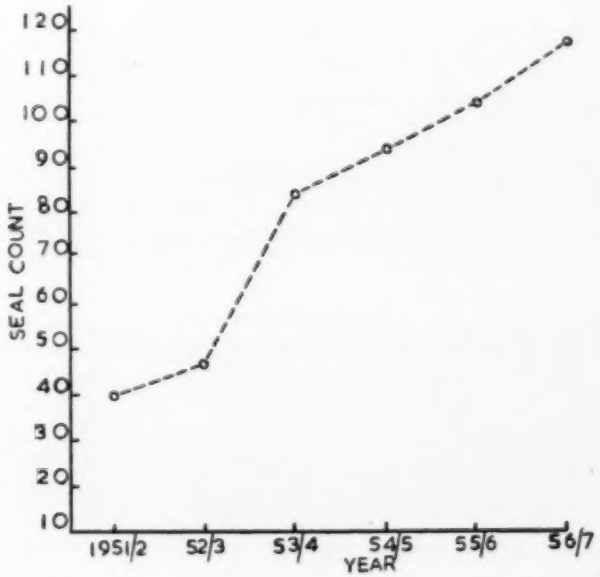


Fig. 4.—Maximum seal counts for the years 1951–1957.

that a true and large increase in the Hilbre colony has occurred between 1951 and 1957. We believe that this is the first set of data produced on the grey seal showing clearly a regular increase in size in a localized group.

Finally, Fig. 5 shows a plot of the counts for 1956–57 for the Hilbre seals

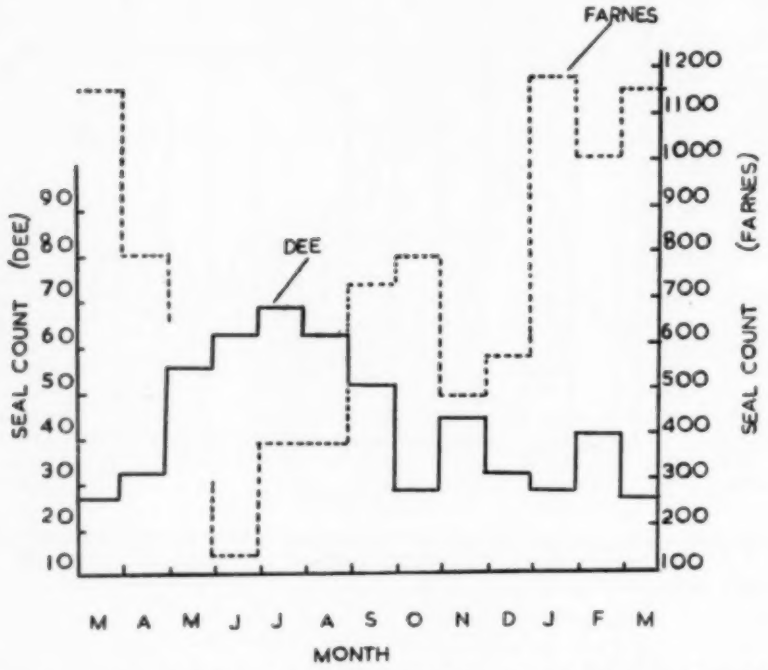


Fig. 5.—Average monthly values for seal counts, Welsh Dee 1951–57 (continuous line); Farne islands 1956–57 (broken line) (from Hickling, 1957).

and for those on the Farne Islands. The rise in population of a breeding colony is of course shown very clearly, and the coincidence of the Farne Islands minimum in and about June with our maximum at about the same time, is striking.

ACKNOWLEDGMENTS

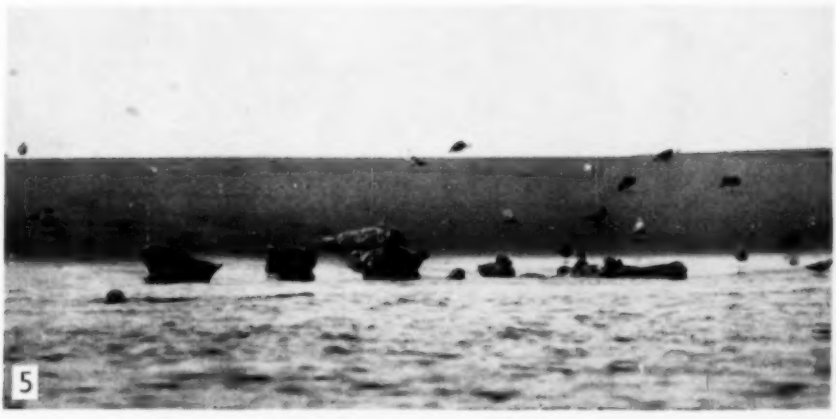
We are most grateful to Professor Hewer for continued advice and most detailed constructive criticisms. Our discussion of the annual cycle of population changes owes a very great deal to him.

We are also indebted to Professor R. J. Pumphrey, F.R.S. for his interest in the observations and for commenting in detail on the first draft of the paper. Mr Eric Hosking, F.R.P.S. has very kindly given us permission to reproduce his photographs (Plate 2, figs. 4 and 5). We are also grateful to Mr Clifton, the Hilbre warden, for many valuable observations and for his

Fig. 1.—The haul-out on West Hoyle Bank, seen from Hilbre Island, across the Swash.

Fig. 2.—Another view.

Fig. 3.—An enlargement of a photograph similar to Figs. 1 and 2. The typical profile of the grey seal can be clearly seen on several seals.



Figs. 4 & 5.—Two photographs taken by Mr. Eric Hosking from a boat on October 1st, 1956. Fig. 4 is of a solitary bull. Note the presence of numerous herring gulls.

courteous help over many years, and to Mr W. Wilson, Mr J. Gittins and others for further data and assistance of all kinds.

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A STUDY OF THE COAT OF THE MOUFLON *OVIS MUSIMON* WITH SPECIAL REFERENCE TO SEASONAL CHANGE

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(With 3 plates and 2 figures in the text)

Changes in the coat and skin of a mouflon sheep were followed from the age of three months to the age of twenty-one months. The birth coat was shed between four and six months of age and there was a marked moult the following spring. During both these moults the coat was lost as a single mat. The wool of the under-coat was shed only once during the spring moult, whereas the hairs of the outer coat were shed a second time in summer, but this was less obvious than the spring moult.

Details of the histology of the skin and of fibre shedding are given in addition to incidental observations on growth and the horns.

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INTRODUCTION

The main object of this investigation was to determine at what time of the year the wild sheep sheds its coat, and the proportion of individual fibres that are involved, in the hope that the information gained would throw light on fibre shedding in domestic sheep.

Because moulting is usually not evident in domestic sheep, it was believed that wool fibres grow continuously, at any rate in the more highly evolved domestic sheep. The fibre shedding that occurs in some breeds in spring was attributed to poor nutrition in winter. Work on these problems was discussed in a review by Ryder (1958 a).

Many mammals have summer and winter coats which are shed in autumn and spring. Little is known about the exact mechanism of the moult, although recent evidence suggests that it is controlled by change in the length of daylight

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(Yeates, 1954). Duerden (1927) found from observations of the coat alone that the primitive domestic Blackhead Persian breed sheds its coat once a year in spring, the kemps of the outer coat being shed first, but not all at the same time. The entire woolly under-coat moults later and is carried away from the skin as a mat with the new growth of kemps. He found (Duerden & Whitnall, 1930) that in the donkey and cow, too, there is only one marked shedding period, in spring, and that the short summer coat changes into the long winter coat merely by increase in length. In the horse, on the other hand, he found two definite shedding periods, in spring and in autumn.

The extensive use of biopsy samples of skin in recent years, for the study of the population of follicles in the skin, has provided evidence, which was reviewed by Ryder (1957), of fairly high proportions of fibre shedding in domestic sheep. The same techniques have been applied to the wild sheep in the present study.

Previous work with wild sheep

The hairy outer-coat of the wild sheep consists of coarse, bristly, heavily-medullated fibres known as kemps (Duerden, 1929). These grow from primary follicles which are the first to be formed in the foetus, and which are characterized by the possession of sweat glands and erector muscles, in addition to sebaceous glands. (The latinised word 'arrector' is replaced here by the more typically English word 'erector'). The woolly under-coat consists almost entirely of non-medullated (true wool) fibres, with a very few intermediate fibres (Crew & Blyth, 1923) that are medullated over part of their length and therefore named heterotypes (Duerden, 1929). The woolly under-coat fibres grow in secondary follicles, which are formed later than the primaries, and their only accessory is a sebaceous gland. Kardymovic (1936) gave figures of 367·5 and 6 microns respectively as the maximum diameter found in the outer-coat, and the minimum diameter found in the under-coat, of wild sheep.

It is generally agreed that the change to the woolly fleece of domestic sheep has been brought about by a reduction in the number and diameter of the kemp fibres and an increase in the number and diameter of the wool fibres. In the so-called double-coated fleeces of some British mountain sheep, the visible part of the outer-coat is composed of long hairy heterotypes (which can be grown by secondary as well as primary follicles) any kemps present being relatively short. Ryder (1957, 1958 b) made some preliminary observations on the arrangement of the follicles in the skin of wild sheep, and drew attention to the fact that the secondaries lie between the primaries. This arrangement had apparently not been discussed previously, although Frölich, Spöttel & Tänzer (1929) said that the secondaries were between the primaries on both the back and leg of the Mouflon, and they depicted a less extreme arrangement on the shoulder.

MATERIAL AND METHODS

The animal used for the present investigation was a male Mouflon born in London Zoo on the 8th April, 1958, which had been received in Leeds when eleven weeks old. It was left entire and kept in a pen in a stable, the natural

lighting of which was augmented by a fluorescent strip light during the day. The food provided was hay and an oat concentrate mixture with added minerals, as well as occasional greens.

Samples of the coat and the skin beneath were taken monthly from the mid-side position (Carter, 1943). Skin was removed by the snip method (Ryder, 1956 a), and the histological procedures and follicle counting methods were those of Burns (1949, 1953) and Peart & Ryder (1954). Two consecutive samples were taken from one side, and the next two samples were taken from the opposite side, and so on. Vertical as well as horizontal sections were cut from each sample of skin. In addition, the animal was weighed weekly and photographed bi-monthly.

GENERAL OBSERVATIONS

(*a*) *Description and growth*

On arrival the lamb weighed 22 lb., and the height at the withers was 19 inches, the croup being a little higher. The lamb was deer-like in appearance with long thin legs and a long neck, but the tail was only 3–4 inches long, and was often held erect. The points at which the horns were beginning to develop were indicated by displacements of the hair.

The rate of growth was less than in domestic sheep. The increase in body weight is shown in the graph (Fig. 1) and increase in size can be judged from the plates which show the animal against a background of 2 inch squares.

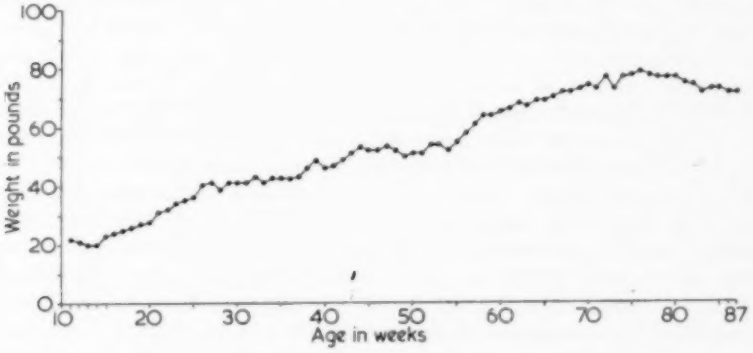

Fig. 1.—Body weight.

The height of the withers at six months was still only 19 inches, but at eight months it had increased to 21 inches. By ten months the height of the withers had increased to about 24 inches, and was similar to that of the croup. At seventeen months it had reached 25 inches, and at nineteen months (November 1959) 26 inches. According to Lydekker (1912) mature rams are about 27 inches at the withers.

The adult central incisors were fully erupted at sixteen months ; they probably appear when the animal is about a year old as in domestic sheep.

(*b*) *Horn growth*

The rate of horn growth, too, was less than in domestic sheep. Small pointed scurs could be felt at three months, and in the next month these became broad and rounded. At five months they were about half-an-inch long, being only a little longer than their width. During the following month the horns increased in length to about three-quarters of an inch, and they had a small peak rising from a broad base. By about seven months they had reached an inch in length, being of definite horn shape, and at nine months the horns were about 2 inches long. Their shape began to show a twist and a fairly sharp bend towards the side of the head at about eleven months, and they were flattened in section. This bend may have been accentuated by the habit of pushing the horns against the side of the pen. The right horn, which did not bend so sharply, was frequently scratched on the salt-lick, and when the animal was almost a year old, the casing of the right horn was lost. This measured 85 mm. (about 3 3/8 inches) along the anterior angle, and had a cavity at the base about 1 inch in depth. The bony core was, however, not as long as this, and it soon became covered with horn again. There were many hairs embedded in the outer part of the horn extending to within about three-quarters of an inch from the tip.

The new horn grew rapidly, becoming about an inch in length within a month, and in two months was almost half the length of the left horn. At about fourteen months, the left horn had bent so much that it was approaching the eye. The tip was therefore sawn off, and the result was that the horns were again of similar length. As the horns were therefore subsequently unnatural, no further descriptions of them will be given.

(*c*) *Coat colour*

A detailed and accurate description of the colour distribution of the coat cannot easily be given. The following is only a general description, which is not necessarily of the standard required by the taxonomist.

The lamb coat (Plate 1a) was on the whole much darker than that grown later. The top of the head and snout, the shoulder, britch and tail were dark brown with a sprinkling of paler hairs. The flank was tinged with pale brown due to hairs whose tips were this colour. Pale brown is perhaps a 'colourless' term to use for this attractive 'ginger' shade of brown. It is used, however, to emphasize the fact, that although the shade varied, it never became as red or as dark as the chestnut colour of the Red deer. This coloration would have been more widespread had not most of the tips been broken off from the shoulder and britch. The sides of the head, the under-side of the ears, and the legs were whitish, and there was a pure white band on the britch at each side of the tail. The belly, too, was whitish and the hairs here were longer than in the adult. Other features, such as the dark band on the anterior aspect of the fore-legs, are visible in Plate 1a.

The new coat grown in August and September, after the birth-coat had shed, was on the whole lighter in shade (Plate 1 b); most parts of the trunk were completely pale-brown, with many white fibres, although the pale brown colour tended to be a little more chestnut than in the lamb. It is of interest

that the lambs of the primitive Loaghtan breed and the modern Suffolk are dark or black at birth and become paler later. Most parts that had been whitish in the birth coat, such as the belly and the under-side of the ears, were now pure white, but the edges of the ears were black. The head remained dark, and some parts of it were even darker than in the lamb. The britch had a whitish tinge, and there was now a black band posteriorly bordering the white area at each side of the tail. The tail itself was now white laterally and ventrally. The black band on the anterior aspect of the fore-legs had become more prominent, and other adult features such as the throat fringe were beginning to appear. This was evident in the anterior part of the chest where it was entirely black ; only later did the throat fringe spread to the throat, where it retained a white patch. Similarly it was October before a black mane became evident on the dorsal aspect of the neck, and before a black band separating the belly from the flank appeared. In October, too, there were many white fibres on the flank, but it was December before the saddle-patch became well defined.

The new coat grown after the spring moult of 1959 was at first pale brown to chestnut in colour, but later became darker, particularly on the shoulder, due to the growth of many new black hairs. By the autumn, most parts anterior to the saddle-patch were quite black (Plate 2 d).

(d) Histological description of the skin

The follicles were disposed at much more acute angles in the skin than in domestic sheep, the angle being more comparable with that found in mice and deer. Wildman (1932) noted that the follicles of hair-bearing areas in domestic sheep had a greater ' slant ' than the follicles in wool-bearing areas.

This primitive arrangement of three primaries and their associated secondaries was more common than in domestic sheep. The central primary of the trio was larger than the two lateral ones, and the secondaries were grouped between the laterals and the central. The first two secondaries of the group to be formed between the primaries, which with the primaries form a typical ' five-group ' (Ryder, 1956 b), were frequently distinguishable even in the adult. The fibres growing in these two follicles often had more pigment than those of the remaining secondaries.

In sections cut at a level not far below the skin surface, two or three secondary fibres were often seen within a single follicle lumen. These correspond to the compound follicles described by Auber & Ryder (1956) and may indicate that the later-formed secondaries develop by branching from those developed first as observed by Hardy & Lyne (1956) in the Merino. One factor which makes the separation of the primaries by the secondaries in wild sheep more marked is the large size of the primaries. They extend such a relatively long distance from the ental side of the group that they readily embrace the much smaller secondaries between them. In this animal, the secondaries were not entirely between the primaries, as depicted by Ryder (1957, 1958 b), but formed a wedge grouping as depicted by Frölich, Spöttel & Tänzer (1929) in which little more than the point was between the primaries (Plate 3b). Lack of space precluded the mention by Ryder (1958 b) that not

all the samples examined had groups with the secondaries between the primaries ; some had this wedge grouping instead. It was thought that the difference was due to skin shrinkage, which is more likely to push the secondaries from in between, than to cause them to appear between, the primaries. Since the grouping varies in different parts of the body, the position of the sample is important. Carter (1943) showed that on the leg of the Merino the secondaries were between the primaries ; one would expect such a hairy region to have the more primitive follicle arrangement.

Although it is possible that some of the samples from museum skins examined by Ryder (1958 b) might have had a different grouping because they were sampled at the edge, i.e. from the belly, or the leg (where it seems that the extreme condition is found) the specimen depicted by Ryder (1957) showing the extreme condition was in fact from the mid-side position. In the present study one sample was taken from the belly of the Mouflon (August 1959), and although the secondaries tended to be further between the primaries than in the mid-side position, there was no marked difference in grouping.

When Ryder (1958 b) described the follicle arrangement in some skin from (the belly of) a stuffed Mouflon × Soay sheep that had been one of Professor Cossar Ewart's experimental animals (Ewart, 1919) it was not expected that another specimen from this cross would be readily available. Then Professor T. Grahame of the Royal (Dick) School of Veterinary Studies, Edinburgh, sent some skin from a Mouflon × Soay ram he had killed. In this, the follicle grouping was very like that in the Soay, whereas the first sample examined, having secondaries between the primaries, was more like the Mouflon parent. Although the grouping in the first specimen may have been merely characteristic of the body region, here there is the possibility that in crosses one animal may resemble one parent, while another animal may resemble the other. The ratio of the number of secondary follicles to the number of primaries (S/P) of this animal was 4·9 on the shoulder and 3·8 on the britch.

Counts made of a few follicle groups in the samples examined by Ryder (1958 b) showed that the ratio of most of the specimens from wild sheep was about 4/1. But in one specimen (Argali) it was about 5/1, and in another (Red sheep : *O. orientalis*) it was 6/1. The S/P ratio in the present animal was determined from full-scale counts, and ranged from 4·0/1 to 6·8/1 with a mean of 5·21/1, in the sixteen samples taken up to September, 1959. There did not appear to be any difference between the sides of the body, and the variation found (Table 1) was apparently mainly due to the slight differences in sampling position. The lowest values were, however, obtained during periods of fibre shedding, and this was no doubt because, having been retracted towards the skin surface during the shedding process, a number of secondaries were entirely above the level at which the count was made.

The bilateral nature of the fibre, now well established in many fine-woolled domestic sheep (Ryder, 1959 a), was clearly shown by the woolly under-coat of the Mouflon studied in the present investigation. The wool fibres were keratinised asymetrically, and the demarcation between the two sides was frequently straight as in Merino fibres. In addition, the pigment was more dense on one side of the fibre than the other, as found in pigmented wool fibres

from domestic sheep such as the Welsh Mountain, and in animals such as the Vicuna (Laxer, Whewell & Woods, 1954). The primary fibres, on the other hand, were apparently keratinised concentrically, which accords with their being more straight than the secondary fibres.

The primary fibres usually had a wide latticed medulla (Wildman, 1954), and the secondary fibres were non-medullated. There were on the whole few non-latticed medullae ; a narrow non-latticed medulla was very occasionally found in a secondary fibre, and also occasionally in the primary fibres when they were narrowing in the fibre shedding process preparatory to the formation of a brush end. But the narrowing and loss of latticed medulla before shedding was usually far more abrupt than in domestic sheep, where it is usual for a latticed medulla to become non-latticed before it disappears altogether.

A few unusual fibres were seen in the sample taken at three months of age (Plate 3 a). These had a central solid part completely encircled by a latticed medulla. The surrounding cortex gave the normal staining reaction of a fully-keratinised fibre, and the latticed-medulla had the usual stain. The central solid part was green with traces of nuclei, like un-keratinised cortex, and in the middle of this was a pigmented portion. The part within the medulla therefore appeared to be cortex rather than unusual medulla, and tracing of serial sections showed that at a higher level this disappeared and gave rise to a normal latticed medulla. At a lower level the central solid part acquired a keratinised rim, and at a still lower level this rim became continuous with the surrounding cuticle and cortex. The fibre appeared U-shaped in section and only a small part of the central solid part remained with the U. It is not clear how this abnormality had arisen, but it appears from this termination to have originated as an invagination into the medulla. The puzzling aspect of the structure is that the less differentiated portion of the central solid part lay at a more proximal level than the more differentiated (keratinised) portion.

I am grateful to Dr L. Auber for examining a similar abnormal fibre in the sample taken in October 1959. He considers this to be an instance of fibre branching similar to that described by Auber & Ryder (1956). In this a fully keratinised fibre with a latticed medulla appeared gradually to invest (in a distal direction) an un-keratinised fibre, which also had a latticed medulla and was in the same follicle lumen. In fact, as in the abnormality described above, the un-keratinised fibre originated as a solid cortical strand within the latticed medulla of the other. Below this, in the region of branching, the keratinised fibre was U-shaped in section and embraced the un-keratinised fibre within the U. At the base of the U, where the two fibres were joined through their latticed madullae, medullated cells were intermingled with cortical cells that were continuous with the cortical strand above. At a still lower level, the two fibres appeared distinct, the one that had apparently come from within the other being un-keratinised.

(*e*) *The histology of fibre shedding*

The shedding process in the Mouflon seems to be essentially similar to that in other mammals including domestic sheep. The fibre narrows and

ceases to produce a medulla, and the pigment disappears, above the skin surface, and a keratinised ' brush ' is formed at the root end (Plate 3 b and d). The follicle becomes shorter, being retracted towards the skin surface, so that the brush is formed at about the level of the attachment of the erector muscle, which appears to remain a similar length to that when the fibre is growing. The bulb, which is virtually the only part of the follicle remaining below the erector muscle attachment, and the papilla, shrink in size, until they are much narrower than the brush lying immediately above them. The papilla, however, occupies a relatively large proportion of the volume of the bulb as compared with the papilla of an active follicle, and its shape has been likened to that of an egg cup by Burns & Auber (1951).

The inner sheath of the fibre is lost so that the fibre is held in the follicle only by the brush, the ' bristles ' of which interlock with a green-staining mass which replaces the inner sheath at the brush level (Plate 3 d) and which gives a strong reaction for thiol (SH) groups. A characteristic of shedding follicles is that the nuclei of the cells in the outer layer of the outer sheath become prominent and elongated with the long axis pointing towards the centre. This seems to occur early in the shedding process because in the second of the Mouflon × Soay samples mentioned above many of the follicles had this appearance although few brushes were evident. The inner sheath on the other hand is lost late in the process.

The network of blood vessels around the follicle is reduced (Ryder, 1956 c) so that capillaries remain only around the shrunken bulb, which is the main part to retain any pigment. The bulb is of course the part of the follicle that remains dormant to give rise to a new fibre to replace the old one.

An important difference from domestic sheep is that it was commonly found in the Mouflon that the new fibre grew before the old one had fallen out. The new fibre grows on the ectal side of the follicle, i.e. the side opposite to the erector muscle attachment (Plate 3 a) and its tip is heavily pigmented (see fibre descriptions below) which seems to be a characteristic of vigorous fibre growth. This regrowth before the old fibre has shed was also found in the Soay sheep examined by Ryder (1959 b) and is similar to the growth in rats and mice, in which two or more fibres with brushes, as well as a growing fibre, are often seen in the same follicle. The growth of a new fibre before the old one has shed may be a mechanism designed to ensure that at no time is the animal naked. A regrowing primary fibre was seen in the present study to have burst through the follicle wall and was growing free in the connective tissue, *cf.* Auber & Ryder (1956).

In domestic sheep, on the other hand, it is rare for a new fibre to grow before the old one has shed. In fact bald patches are sometimes seen from which the wool has been lost and not yet begun to regrow. The author examined skin from one of these areas in a Teeswater sheep and found that the lumen of each follicle was almost blocked with stratum corneum. Many follicles, however, still had a brush, and often an appreciable length of fibre remaining within the stratum corneum, which suggested that the fibres had broken off above the brush rather than being shed. The green-staining mass around the brush was continuous with the stratum corneum at higher levels

of the follicle, whereas this does not normally extend above the brush (Plate 3 d). Although the sweat glands were apparently normal, the cells of the sebaceous glands were in an undifferentiated state whereas the sebaceous glands usually appear to remain active during the shedding process (Plate 3 d).

OBSERVATIONS OF CHANGE IN THE COAT

The first sample was from the birth-coat. This was taken when the Mouflon lamb arrived in **June 1958** at an age of about three months. The woolly under-coat was about 10 to 15 mm. long, the wool fibres being curly, and grey in colour. The hairs of the outer-coat were about 30 to 35 mm. long ; the tips were sharply pointed and were straight and black for the first 1 mm. Following this the hairs had a shallow wave which continued right down to the skin surface. The next region below the black tip, about 6 mm. long, was pale brown in colour. Below this, the fibres were dark brown to black for the remainder of their length, although a few again became pale brown at the base.

Many of the hairs became narrower for a length of 5 to 10 mm. at a level not far below the termination of the pale brown region. On the shoulder and britch most of the tips, i.e. roughly the first 10 mm. of the hairs had broken off at this narrow point, so that these areas appeared darker than the flank (Plate 1 a). These fibres are perhaps analogous to the halo-hairs (Dry, 1933 a) found in the birth-coats of some domestic sheep. It is of interest that a few other hairs resembling curly-tips (Dry, 1933 b) were found. These were darkly coloured for the whole of their length ; they had a fairly curly tip, and were of only medium diameter, i.e. less than that of the other hairs. It seemed possible that these might have been the forerunners of the heterotypes described by Crew & Blyth (1923) in *O. vignei*, but no heterotypes were found in the adult coat of the present animal. I am indebted to Dr F. W. Dry for examining the fibre type array of this sample which was taken rather late for this purpose. He found that it was of saddle type and exhibited a primitive pre-natal check as found in other Mouflon material by Dry & Stephenson (1954).

There were some coarser hairs that were only about 20 mm. long ; these were apparently adult fibres that were replacing birth-coat hairs that had already shed. The black tip of these hairs was longer (5 mm.) and more slender than that of the birth-coat hairs and below the tip was a white region about 10 mm. long. Below this the remainder of the fibre was dark brown to black. It is possible that these fibres had a white, instead of pale brown, band because the sample was taken from the area that later became the white saddle patch.

Examination of horizontal sections cut from the skin sample showed typical trios of primary follicles (Plate 3 a). The lateral fibres were on the whole either non-medullated or ended in a brush preparatory to being shed, whereas many of the fibres of the central primaries had large latticed medullae occupying most of the width of the fibre. These were no doubt the replacement fibres that had been seen in the coat sample (above).

A follicle count made at the level of the sebaceous glands, the level at which the follicle grouping is seen best, showed that 40 per cent of the primaries

had a latticed medulla, 45 per cent had no medulla, 13 per cent had a brush end, and 1 per cent had a non-medullated fibre growing alongside a brush to replace the old fibre after it had shed.

In order to obtain a more accurate estimate of the number of follicles shedding their fibres, a second count was made in a section cut at a lower level. In this, the proportion of fibres with a latticed medulla was similar (39 per cent) in accordance with the observation (above) that when a fibre loses its medulla prior to shedding, it does so above the skin surface. On the other hand, the proportion of non-medullated fibres had dropped from 45 per cent to 9 per cent, and this was associated with an increase in the proportion of fibres with a brush from 13 to 51 per cent (Table 1).

Most of the fibres with a latticed medulla were fairly heavily pigmented, whereas few of the non-medullated fibres (about to shed) had any pigment at all. Some follicles with a fibre ending in a brush had a little pigment in the outer sheath. The narrow, non-medullated replacement fibres were densely pigmented, corresponding to the black fibre tip.

The majority of the secondary follicles had fine non-medullated fibres, but there were a number of plugs of undifferentiated tissue. A group of these were traced in order to determine whether they belonged to developing or shedding follicles, and in fact they were all found to be part of a sebaceous gland. The count showed that 1 per cent of the secondary fibres had a brush end.

At three months of age therefore, follicle development was complete, and the birth-coat was beginning to shed, the outer-coat being at a more advanced stage of shedding than the under-coat.

At the end of **July 1958** the appearance of the coat was the same as when previously sampled, at the end of June, but individual hairs were shedding freely. The coat sample was similar in length and appearance to the previous sample, but there were apparently a greater number of coarser replacement hairs. These had black tips, and many were white down to the skin surface, closely resembling kemps from domestic sheep. There were some other replacement hairs which had similar black tips, but which were less coarse and pale brown in colour.

A follicle count made from the skin sample showed that a similar proportion of the primary fibres (40 per cent), to the last sample, had a latticed medulla (Plate 3 b). There were fewer (47 per cent) primary fibres with brush ends, and more fibres (13 per cent) with no medulla, but 27 per cent of these were narrow and densely pigmented, showing them to be tips of replacement hairs. In this sample 75 per cent of the secondary fibres were in the brush stage of shedding, the remainder being non-medullated. Only 5 per cent of the total were pigmented, and the pigment was only sparsely distributed.

During the early part of **August 1958** the coat began to peel away in a single mat, and from the middle of the month until the beginning of September large masses of outer hair, with finer wool rubbed into balls among it, could be readily plucked off. The August fibre sample comprised the new coat only. This was 15 to 20 mm. long, and the woolly under-coat was not very evident. The white hairs (and some all black ones) were now the longest and

coarsest fibres. Most of the hairs were as yet no coarser than those of the birth-coat and below the usual black tip they were pale brown for about 10 mm., below which they became dark brown for the remainder of their length.

Examination of the skin sample showed that the central primaries still had a large latticed medulla which had increased in diameter since the last sample. Many hairs appeared irregular in cross section as found in some hairy domestic sheep such as the Scots Blackface. The proportion of primary fibres with a latticed medulla had increased to 43 per cent. But 25 per cent of the primaries still had fibres ending in a brush, although 5 per cent had a new fibre growing alongside a brush. The proportion of fibres with no medulla had increased to 27 per cent, and the proportion of these that were pigmented, and therefore replacement fibres, had increased to 35 per cent. Some of these had in fact begun to produce a medulla again, but as yet it was narrow and non-latticed. Only 20 per cent of the secondaries were now shedding their fibres (possibly the ones that had not been shedding in the July sample). The remainder had non-medullated fibres ; many of these were sparsely pigmented suggesting that they were new fibres replacing those that had shed.

During **September 1958** there was still a lot of the dark brown birth-coat remaining on the shoulder (Plate 1 b). The new hair on the neck and the hip was pale brown to chestnut and when this was parted no wool could be seen. The first traces of a white saddle patch were visible on the flank. The coat sample was about 30 mm. long with tips of the longer white, and black hairs extending nearly 10 mm. above the rest of the coat, which was otherwise similar to the last sample. Although not very evident, some wool could be seen at the base of the staple.

There were no shedding follicles in the skin sample, showing that the shedding of the birth-coat was complete. The lateral primary fibres were narrower than the centrals, but the majority had a wide latticed medulla ; only a few had a narrow non-latticed medulla (Table 1). A few of the primary fibres appeared irregular in section, being either flattened or V-shaped, and 85 per cent were pigmented. All the secondary follicles had fine, non-medullated fibres and many were sparsely pigmented.

At the end of **October 1958** there was still a mass of wool from the birth-coat matted in the tips of the new hairs. In fact this wool remained until the hairs themselves were shed the following spring. The white saddle patch was more evident, but little new wool could be seen when the hairs were parted. The coat sample was about 40 mm. long, with the tips of the longer white (and a few black) hairs again extending about 10 mm. above the rest of the coat. The basal 15 to 20 mm. of each hair, except the black and white ones, was dark brown to black, and this part of the staple was now densely packed with apparently grey wool fibres about 15 mm. long, which were obvious in the sample although not easily seen in the fleece.

In parts of the skin sample, the primaries had begun to form brushes again. Distortion of the sections made it impossible to tell whether the centrals or laterals were shedding, but 3 per cent of the primary fibres were

TABLE 1

Percentage of the different follicle types found in the monthly skin samples.

	Primary follicles							Secondary follicles						
	Latticed Medulla	Non-Latticed Medulla	No Medulla	Brush	Shed Empty	Shed Regrowing	Disrupted	Non-Latticed Medulla	No Medulla	Brush	Shed Empty	Shed Regrowing	Lymphatic	S/P Ratio
Date														
27/ 6/58	39	–	9	51	–	1	–	–	99	1	–	–	–	4,1
29/ 7/58	40	–	13	47	–	–	–	–	25	75	–	–	–	4,0
26/ 8/58	43	–	27	25	–	5	–	–	80	20	–	–	–	4,1
30/ 9/58	99	1	–	–	–	–	–	–	100	–	–	–	–	6,0
28/10/58	59	–	3	10	–	–	28	0·4	98·6	–	–	–	1	5,6
25/11/58	53	1	12	34	–	–	–	0·1	99·9	–	–	–	–	6,8
23/12/58	5	–	56	34	3	2	–	–	100	–	–	–	–	5,4
27/ 1/59	–	–	–	100	–	–	–	–	100	–	–	–	–	5,4
24/ 2/59	39	–	–	47	5	9	–	–	96	4	–	–	–	6,0
21/ 3/59	65	–	–	31	–	4	–	–	95	5	–	–	–	5,1
27/ 4/59	70	–	18	6	–	6	–	–	95	4	–	1	–	4,7
2/ 6/59	35	–	55	10	–	–	–	–	64	9	25	2	–	4·6
23/ 6/59	44	9	24	4	3	16	–	–	74	1	24	1	–	4·6
27/ 7/59	92	–	6	–	–	2	–	0·5	98·5	–	1	–	–	5·0
31/ 8/59	80	–	14	5	–	1	–	–	100	–	–	–	–	5·7
29/ 9/59	90	–	10	–	–	–	–	–	99	–	–	1	–	6·1
26/10/59	52	–	48	–	–	–	–	–	100	–	–	–	–	5·9
27/11/59	37	–	63	–	–	–	–	–	100	–	–	–	–	5·5
24/12/59	1·5	–	–	97	–	1·5	–	–	99	1	–	–	–	5·5

non-medullated and 10 per cent ended in a brush. The proportion with a latticed medulla was 59 per cent, but in this sample 28 per cent of the primaries were disrupted (Plate 3 c). Tracing of serial horizontal sections, and examination of vertical sections showed that the disruption had arisen from the pulling out of fibres either before or during the removal of the skin. The lumen of some of these damaged follicles contained lymph, and this suggested that the three lymphatic (Auber & Ryder, 1956) secondary follicles found, might have arisen in the same way. Most of the secondary fibres were actively growing and non-medullated, but one follicle had a fibre with a small non-latticed medulla. The secondary fibres had a little more pigment than in the previous samples, but this was far less densely distributed than in the primaries.

During August, September and October, the hairs of the new coat grew about 10 mm. each month but by the end of **November 1958** the coat was about 45 mm. long and so had grown only about 5 mm. during the month. The part in question, the lowest 5 mm. of the staple, had begun to lose its pigment, so that this part of each hair was grey to white instead of being dark brown. The wool was dense and extended about 20 mm. up the staple.

Examination of the skin showed that 34 per cent of the primaries ended in a brush, 1 per cent had a non-latticed medulla, and 12 per cent had lost their medulla and pigment completely preparatory to shedding. The proportion that still had a latticed medulla was 53 per cent but only 22 per cent were pigmented. All of the secondary follicles had an actively growing fibre, two had a non-latticed medulla (0·1 per cent), but only 6 per cent had any pigment.

The length of the staple at the end of **December 1958** was about 50 mm. so that it had again grown only about 5 mm. during the month, and the lowest few millimetres were definitely white. The wool was about 25 mm. long, and it, too, was white at the base of the staple which accorded with the observation from the skin of the last sample that fewer of the secondary fibres were pigmented.

Only 5 per cent of the primaries had fibres with a latticed medulla, 56 per cent of the fibres had no medulla and 34 per cent ended in a brush. Two follicles (3 per cent) in the shedding stage had lost their fibres, and one follicle (2 per cent) had a fibre growing to replace one that had shed. All the secondaries had actively growing fibres, and these had less pigment than in the last sample.

By the end of **January 1959** (Plate 1 c) the coat sample was similar in and appearance to the last sample, but some hairs were 55 to 60 mm. long, and the wool was 30 mm. long. The skin showed that all of the primary fibres had a brush end, whereas all the secondary fibres were actively growing.

During **February** many, but not all, of the hairs were so loose that stroking, or gentle pulling, would remove them. The coat was of similar length to the last sample, although the under-wool had increased in length to 35 mm. The shed hairs were 50 to 60 mm. long and had a tapering black tip 2 to 5 mm. long. In some hairs the black colour persisted until the pigment began to be lost about 10 mm. from the base, but most had a white or pale chestnut band about 5 to 15 mm. long immediately below the black tip. Hairs that

were flattened in section (ribbon-like) were crimped in the plane of flattening only. Those that were circular in section had the usual spiral crimp.

The skin sample showed that 39 per cent of the primary follicles had fibres with a latticed medulla. These fibres must have all commenced to grow since the previous skin sample was taken, but they were not evident in the February fibre sample. There were 9 per cent with narrow, non-medullated, but heavily pigmented, fibres growing to replace shed hairs, and most of these were alongside the brush of the old fibre ; 5 per cent of the primaries had shed their fibres and had an empty lumen, and 47 per cent still had fibres ending in a brush. Only 4 per cent of the secondary follicles had fibres ending in a brush.

In the second week of **March** the whole coat began to peel away as a mat from the sides of the neck (Plate 1 d) and individual hairs still continued to be shed freely. The coat sample was still the same length as before, but the wool had increased in length to 40 mm. and was very dense and obvious, possibly owing to the loss of hair. Although the wool fibres were as fine as those of the Merino (they were judged to be 70s quality by a wool buyer) they had a loose curl with a wavelength of about 1 mm. as opposed to the tight crimp of the Merino. There were many new hairs from a few millimetres to 20 mm. long ; some were all black, but others were black only at the tip as before.

Examination of the skin showed that 38 per cent (a similar proportion to the last sample) of the primary fibres had a large latticed medulla ; a further 27 per cent had a small latticed medulla and were clearly new hairs, while 4 per cent were new fibres that had not yet acquired a medulla. There were still 31 per cent ending in a brush. The proportion of secondary fibres ending in a brush had not increased significantly from the last sample (Table 1) despite the fact that the wool had begun to shed from the neck.

During **April** the old coat was lost from the dorsal part of the neck, and from that part of the chest anterior to the fore-legs. The anterior edge of the old coat was too firmly held to be pulled out. The fibre sample showed that the coat (mostly wool) was now about 50 mm. long ; all the old hairs seem to have been lost (particularly from the side of the body) and the new hairs were about 30 mm. long. These included black ones, white ones with black tips (saddle patch) and pale chestnut ones. The wool was denser above the tips of the new hair, and although many wool fibres were continuous down to the skin, it appeared that many had shed. The skin sample showed that 70 per cent of the primary fibres had a latticed medulla, and that 6 per cent were non-medullated and pigmented, being therefore replacement fibres. There were 6 per cent ending in a brush, which were probably fibres from the old coat that had not yet shed, and although some of the 18 per cent with no medulla and no pigment may have been from the old coat, it is likely that they were fibres from the new coat that had already completed their growth cycle. Although from the fibre sample it appeared that much of the wool had shed, 95 per cent of the secondary follicles were still actively growing in the skin.

By the middle of **May** (Plate 2 a), the old coat had been shed as far as the withers, and was beginning to be lost from the lower part of the trunk. By

the end of the month it had been lost completely from this part of the trunk, and the hind-quarters, so that the May sample was from the area of the new coat, which was 30 to 35 mm. long. The hairs had a tapering black tip 2–3 mm. long following which the fibres broadened and became white or pale chestnut in colour for a length of about 8 mm. The remainder of the fibre was dark brown to black. Some fibres, below the black tip, were all white, all chestnut or all black. The chestnut fibres were more slender than those that were completely black or white. As after the shedding of the birth-coat, little wool was evident at the base of the staple.

The skin showed that the proportion of primary fibres with a latticed medulla had dropped to 35 per cent, and that the number with no medulla or pigment had increased to 55 per cent. These therefore appear to have completed their growth cycle (vertical sections showed loss of medulla) and this is supported by an increase in the proportion of primary fibres with a brush end from 6 to 10 per cent. Yet the length of the coat was no greater than 35 mm. Only 64 per cent of the secondary follicles had actively growing fibres, and the proportion with fibres ending in a brush had increased to 9 per cent. There were 25 per cent that had shed their fibre, but not yet grown a new one, although 2 per cent had replacement fibres. Many of the ' empty ' follicles had the remains of a brush and tracing towards the skin surface showed that the fibre had broken off within the follicle.

This sudden increase to almost 40 per cent of the secondaries at some stage of shedding must have occurred within the last month. There is no question of brushes having been missed previously. Examination of the lower levels of the February, March and April skin samples showed that the majority of the secondary fibres had a normal keratinisation region. The lumen of the secondary follicles without fibres was filled with a streaky pale green mass, similar to, but paler than stratum corneum. These were therefore comparable with the ' empty ' follicles in the Teeswater described above. The lumen of some of the follicles contained large, round black nuclei comparable with those in the multinucleated tissue of certain lymphatic follicles (Auber & Ryder, 1956).

At the time of the **June 1959** sample, little more of the old coat had been lost, and a fibre sample taken from the shoulder (Plate 2 b) showed that the old wool was firmly matted in the hair of the new coat. The fibre sample from the mid-side was of similar length (35 mm.) and description to the May sample, the wool still being not very evident and the length not clear. It is noteworthy that whereas the hairs of the mid-side had their usual pale band near the tip, those on the shoulder were either completely chestnut or completely black.

The skin sample showed that the proportion of primary follicles with a non-medullated fibre had dropped to 24 per cent and the proportion with a latticed medulla had increased to 44 per cent, about one-quarter of these being heavily pigmented. The proportion having fibres with a brush end had decreased to 4 per cent, but 3 per cent were ' empty ' after having shed their fibres. There were 16 per cent with fibres replacing others that had shed, and a further 9 per cent had fibres with a non-latticed medulla, that were clearly

replacement fibres, too. The proportion of secondary follicles with fibres that were actively growing had increased to 74 per cent, and about one-third of these were appreciably pigmented suggesting that they were replacement fibres ; 1 per cent clearly had replacement fibres and there were still 24 per cent with no fibres, but the proportion having fibres with a brush end had decreased to 1 per cent.

By the middle of **July 1959** (Plate 2 c) a fair amount of the old coat still remained on the back. There was a black throat fringe, and a black mane on the dorsal part of the neck. These were better developed than in the coat grown after the birth-coat had shed, and the hairs were longer than the rest of the coat which was chestnut. The fibre sample from the mid-side position showed that the hairs were about 40 mm. long, and that the wool was about 10 mm. long.

From the skin it was seen that the proportion of primary follicles with a latticed medulla had increased to 92 per cent, and the proportion with no medulla had decreased to 6 per cent. The proportion with replacement fibres had decreased to 2 per cent (one follicle). The proportion of secondary follicles with an actively growing fibre was 98·5 per cent, there were 1 per cent (three follicles) that were ' empty ' after having shed their fibres, and 0·5 per cent (one fibre) with a non-latticed medulla. This follows the logical sequence of a completion of the spring shedding of the secondaries, and the completion of a second wave of shedding in the primary follicles with a peak in May.

Early in **August 1959** a sample was taken from the belly in order to examine the follicle arrangement in that region. The fibres from this part were mostly completely white, with a few all black ones that were paler towards the base indicating that they were completing their growth cycle ; yet they were only about 10 mm. long, whereas this had been the longest part of the coat in the lamb. The skin confirmed that these fibres were completing their growth cycle (not in Table 1) ; only 3 per cent of the primary fibres had a latticed medulla, 1 per cent had a brush end and 96 per cent were non-medullated, but examination at a lower level showed that most of these in fact had a brush end. There were 15 per cent of the secondary fibres with a brush end, and one secondary fibre with a non-latticed medulla, the remainder being actively growing non-medullated fibres.

At the end of August 1959 there was still an area of the old coat extending over the loin from the anterior border of the saddle patch. In fact much of this remained until after December when the present series of observations were finished (Plate 2 d). It seems likely that many of the wool fibres of the old coat were continuous down to the skin surface. The fibre sample showed the hairs to be still only about 40 mm. long, and the wool to be about 10–20 mm. long. Although stroking or gentle pulling caused a few hairs to come out, suggesting that shedding had commenced again, the skin showed that the proportion of primary fibres with a latticed medulla had decreased only to 80 per cent from the July figure of 92 per cent. The proportion of non-medullated primaries had, however, increased to 14 per cent, there were 5 per cent with a brush end, and the proportion of replacements was 1 per cent (one fibre). All the secondary follicles had actively growing fibres.

The sample taken in **September 1959** showed that the hairs were about 50 mm. long, and that the wool was 20 to 30 mm. long. The skin showed that the proportion of primary follicles with a latticed medulla was 90 per cent ; this is similar to the July figure of 92 per cent suggesting that the lower value found in August was due to variation in the sampling position ; 10 per cent of the primaries were non-medullated. There were 99 per cent of the secondary follicles with actively growing fibres, and, as in July, 1 per cent were ' empty '.

At the end of **October 1959** the coat appeared thick and healthy, and was relatively greasy. Most of the hairs in the fibre sample were 50 to 60 mm. long, but a moderate proportion of the all-black ones were as much as 75 mm. long. These had spread into the coat from the mane that extends posteriorly along the mid-dorsal line, and were the longest hairs yet found in the coat. The wool was now about 30 mm. long. The skin sample showed that only 52 per cent of the primary follicles had fibres with a latticed medulla, the remainder were non-medullated, and examination at lower levels showed that these ended in brushes.

Although no obvious autumn moult took place, there was a marked change in the coat which can be seen in the photograph taken in the middle of **November 1959,** shown in Plate 2 d. This change was mainly brought about by the growth in length of the black hairs already mentioned, but the white saddle patch became more prominent as it did the previous winter. The black hairs were longest in the chest region and there was a well-developed throat fringe (Plate 2 d). The November fibre sample taken immediately anterior to the saddle patch showed the black hairs (which apparently formed roughly half the total) to be about 120 mm. long ; the remainder of the hairs, which were chestnut (now darker than in the summer) were only about 60 mm. long, i.e. the maximum length reached by the coat the previous winter. Many of the hairs had a pale basal part showing them to be completing their growth cycle, but the long black ones were mostly black down to the skin surface. The wool, more evident now, was about 40 mm. long.

The skin sample showed that 37 per cent of the primary follicles had fibres with a latticed medulla ; these were mostly central primaries, so it seems from the above evidence that the long black fibres were growing from the central primary of the trio groups. The proportion of primary follicles which had a fibre with no medulla was 63 per cent and these were almost all laterals, and the fibres were apparently the shorter hairs of the coat which had a pale basal portion. Examination at a lower level showed that these had a brush end. All the secondary follicles had an actively growing fibre.

During **December 1959** the coat appeared similar to the appearance during the previous month. The sample was taken from the saddle patch, which was immediately posterior to the region with very long hairs, and so the fibres in the sample were mostly only 50 to 60 mm. long with a few black ones 80 to 90 mm. long. There were many white fibres owing to the position of the sample, but even the black ones were white near the base showing completion of the growth cycle. The wool was 40 to 45 mm. long and appeared very obvious. This, too, was longer than in the previous winter, and the most direct explanation for this is that in the second December a longer time had

elapsed from the previous moult, the birth-coat shedding having preceded the first December by only four months.

The skin showed that almost all the primary fibres ended in a brush (97 per cent), but there was one fibre with a latticed medulla (1·5 per cent) and one follicle with a replacement fibre (1·5 per cent). Unlike the previous December a few secondaries had begun to shed, 1 per cent (four follicles) having a fibre with a brush end, and these were in four separate follicle groups, each being one of the first two secondaries to be formed in the foetus. The remainder had an actively growing fibre.

DISCUSSION

The Mouflon has proved to be a useful type of sheep for the study of fibre shedding, because it is obvious from the coat when a moult is taking place, most of the fibres being involved.

In the animal studied, all follicle groups had fibres shedding at the same time, whereas Burns (1953) found in the Scots Blackface that some groups had shedding fibres and others not. The primary fibres did, however, shed before the secondaries (see below) and the centrals were shed at a different time from the laterals. In fact the centrals of the birth-coat had apparently already shed when the observations commenced at three months of age. These are probably similar to the halo hairs of domestic sheep (Dry 1933 a). Roughly 40 per cent of the primary fibres had a latticed medulla in each of the June, July and August 1958 samples when the birth-coat was being shed (the theoretical figure expected if only the centrals had been involved is 33 per cent) and there were shorter, coarser hairs in the June and July fibre samples. Ryder (1956 b) found that shedding had started before birth, and Burns (1953) observed brushes in central follicles, with replacement fibres alongside, in samples taken from new-born lambs.

One advantage of using the Mouflon for this study emerges when considering the autumn months. As with some domestic sheep, fibres with a brush end were seen in the skin samples taken in autumn. But unlike the domestic sheep it was clear that the coat was not being shed. Confirmation was therefore found for the suggestion of Burns (1953) in the Scots Blackface, that the fibres with a brush end seen in the skin in autumn, do not fall out until the following spring.

The rate of growth of the hairs seemed to be fairly rapid ; this is similar to the mouse in which a short growing phase alternates with a long resting phase. The wool fibres on the other hand appeared to grow more slowly. Thus in the first autumn the hairs soon reached their maximum length and formed a brush end, whereas the wool fibres continued to grow throughout the winter, finally becoming as long as the hairs. In this way the coat became relatively more woolly in winter, and the wool was so obvious that it is easily understood how popular statements have arisen about the wool being in fact *denser* in the winter. Conversely, in summer, the wool was surprisingly so difficult to see when the hairs were parted, although skin samples showed all the wool fibres to be growing, that statements about only hair growing in summer can be readily appreciated.

In both the shedding of the birth-coat, and the spring moult, the hairs shed first, doing so gradually over a period. This was followed by the shedding of the wool fibres which occurred during a shorter period, as found in the Blackhead Persian by Duerden & Boyd (1930). The moult passed over the body in the same sequence as observed in the Wiltshire Horn by Slee (1959), i.e. from the anterior and ventral parts first and from the loin last.

There is evidence from a small number of sheep of only a few breeds, that adult domestic sheep that moult have peaks of fibre shedding, as judged from the skin, in spring and autumn. The primary fibres (notably kemps) seem to have a peak in both spring and autumn, whereas there appears to be only one peak of secondary shedding in spring. Wildman (personal communication), however, found an autumn peak of secondary shedding in a group of Romney sheep. The present study has shown that in the Mouflon, at any rate in the first adult year, there is only one complete moult each year, in spring ; this involves both the primary fibres (hairs) and the secondary fibres (wool), but the hairs are shed a second time in summer.

Figure 2 shows the percentages of shedding follicles in the skin as totals of all the follicles at any stage of shedding throughout the period studied. It will be seen that the spring peak of primary shedding in fact appeared in the skin in December and January while the spring peak of secondary shedding

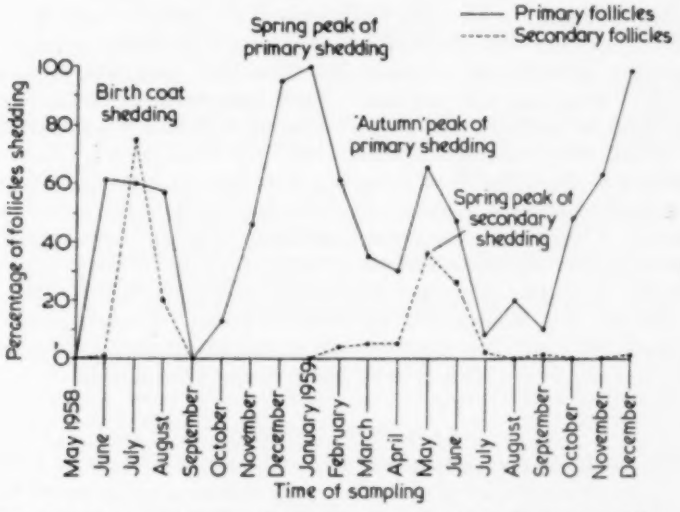

Fig. 2.—Total percentage of follicles in the skin at all stages of shedding.

did not appear until May. Also in May, there was another peak of primary shedding, which had been noted in the monthly descriptions as a second wave. But this was clearly not associated with the secondary shedding occurring at the same time, and it could probably be regarded as an autumn peak of primary shedding. This second peak was, however, not as great as the spring peak and the shedding continued over a longer period. It will be remembered from

the monthly descriptions that hairs were being lost during August, and these were not as long as the hairs in the winter coat. This is the same as in the Herdwick (Burns 1954) and discussion with Miss Burns has suggested that the best terms to use for the two moults are ' winter ' and ' summer '. Duerden & Boyd (1930) thought that hairs in the wild sheep might be lost intermittently throughout the year, and there was in fact only one month (September 1958) in which there was no primary shedding at all. The gradual colour changes in the coat show that replacement hairs are continually appearing at times other than during the moults. Further work is necessary to elucidate this.

A puzzling feature of the spring moult was the slowness with which the old coat was lost. The whole process took from March to July, whereas the author was informed by the keepers that the coat is lost at the zoo fairly quickly during the first two weeks of April. One probable cause of this slowness was that there were no rocks on which the animal probably rubs off the old coat in the wild state, as well as at Regent's Park. But the slowness was also observed in the shedding of the secondary follicles in the skin, which did not appear to shed until the loss of the coat was nearing completion, and which remained ' empty ' for some time after losing their fibres. In fact, although the whole coat was lost, at no time did the proportion of shedding secondaries in the skin reach 40 per cent whereas the proportion reached as much as 75 per cent in one sample taken during the shedding of the birth-coat, and there was evidence that the remainder of the follicles were involved in turn. So it appears that the slowness may have been partly because not all the secondary fibres formed a brush, and those that continued growing must have broken when the coat was lost. There was evidence of fibre breakage even in those secondaries that formed a brush end, and it appears that the animal lacked some stimulus to release the wool fibres with a brush, as well as to make the remainder form a brush. This may have been brought about by the animal being kept indoors. On the other hand, before this is regarded as unnatural it must be remembered that a similar delay in the regrowth of a new fibre was observed in the Teeswater sheep (described in the present paper), and Duerden & Boyd (1930) said that there was a pause between the growth of the old and new wool in the Blackhead Persian. Further work will be necessary to elucidate this problem ; it would be interesting if fibres were found in the Mouflon with a growth phase longer than a year.

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EXPLANATION OF PLATES

The animal was photographed against a background of 2-inch squares.

PLATE 1.

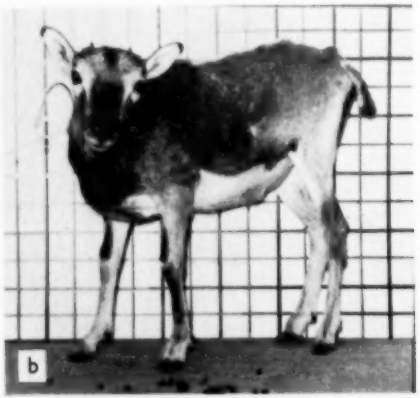
(a) The lamb at about three months of age before the birth-coat had shed.
(b) September 1958 ; six months of age ; some of the birth-coat still remains on the shoulder.
(c) January 1959 ; almost ten months old ; note saddle patch and " woolliness " of coat.
(d) March 1959 ; almost a year old. The coat has shed from the side of the neck.

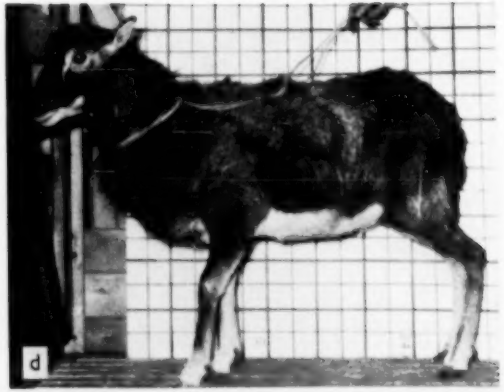
PLATE 2.

(a) May 1959 ; the demarcation between the old and new coats is very obvious.
(b) Fibre sample taken from the shoulder in June 1959 ; the wool fibres of the old coat (top) are firmly held among the tips of the hairs of the new coat (bottom).
(c) July 1959 ; the moult is nearly complete.
(d) November 1959 ; note the long black hairs in the anterior part of the body and that some of old coat still remains on the loin.

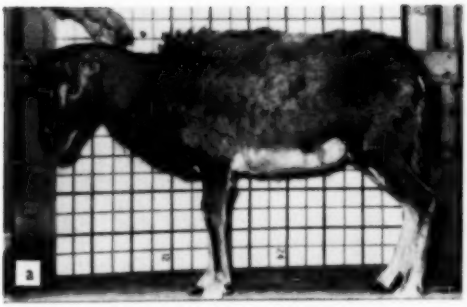
PLATE 3.

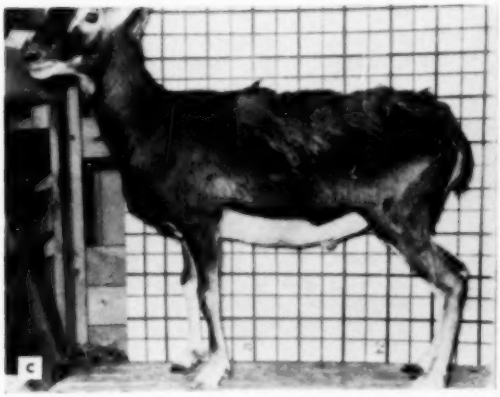
(a) Follicle group in skin taken in June 1958. The first lateral primary (top) of the trio is heavily pigmented, and has a latticed medulla, the central follicle has a heavily pigmented fibre growing to replace one that has not yet shed and the other lateral (bottom) has lost its medulla preparatory to shedding. The fibre at the edge of the section is unusual in having a central solid part within the medulla which is possibly the origin of a branch in the fibre.
(b) More typical primary follicle trio in July 1958 skin sample. The lateral fibre at the top has a brush end, the central is heavily pigmented and has a latticed medulla, and the lateral at the bottom has lost its medulla preparatory to the formation of a brush end. The " wedges " of secondary follicles between the primaries are clearly visible.
(c) Skin taken in October 1958 showing distorted primary follicles (top and bottom) which are thought to have been caused by the accidental pulling out of fibres.
(d) Vertical section of skin taken in September 1959 showing primary fibre with brush end. This has been sectioned obliquely and therefore appears shorter than it really is. Note the lack of inner sheath, the active sebaceous gland, the sweat duct beneath the largest sebaceous lobe, and the erector muscle beneath this.

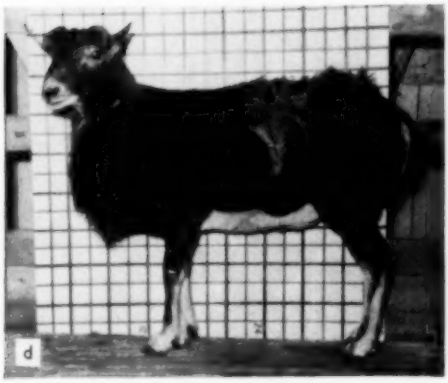




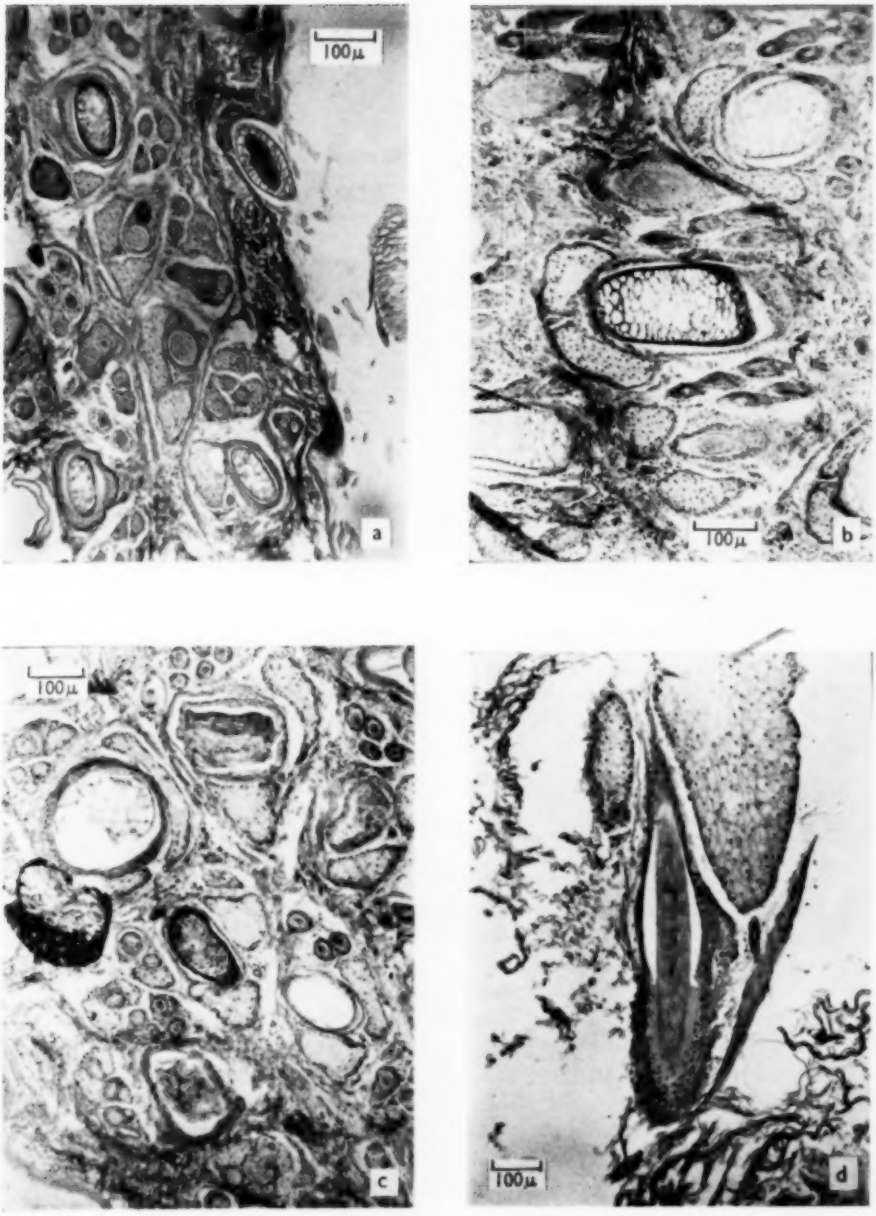
The coat of the mouflon.







The coat of the mouflon.



The coat of the mouflon.

THE SYSTEMATICS, LIFE HISTORY AND EVOLUTION OF THE BANK-VOLE *CLETHRIONOMYS* TILESIUS IN NORTH-WEST SCOTLAND

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[Accepted 9th February, 1960]

(With 7 figures in the text)

Collections of *Clethrionomys glareolus* Schreb. have been made from the mainland of north-west Scotland and the Islands of Mull and Raasay. The skull of the Raasay vole is larger than that of the other two sub-species although the proportions of all three are similar. The number of re-entrants on the inner margin of the third upper molar declines as the tooth wears. On the islands, a higher proportion of newly erupted teeth have three re-entrants.

The three collections differ little in coat colour.

Life expectancy is higher and breeding less intense in north-west Scotland than further south. Comparatively little reproduction is performed by Scottish animals in their first year.

There appears little basis for separating the Mull and mainland subspecies of *Clethrionomys*.

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INTRODUCTION

In addition to the mainland bank-vole (*Clethrionomys glareolus britannicus* (Miller)), two island species have been described from north-west Scotland. Barrett-Hamilton and Hinton (1913 a, 1913 b) described *Evotomys alstoni* from five specimens from the Isle of Mull and *E. erica* from three specimens from the Isle of Raasay. Both species are now looked upon as subspecies of *C. glareolus* Schreber (Matthews, 1952 ; Steven, 1957). Larger overall size, the possession of three re-entrants instead of two on the inner margin of the third upper molar, a darker coat colour and a heavier skull are features distinguishing the island from the mainland voles. The Raasay vole differs from the Mull vole in attaining greater size.

The purpose of the present paper is to re-examine the magnitude of these differences by comparing island collections with those from the adjacent

mainland. Comparisons will also be made of the life-cycle, which can be related to size, in north-west Scotland and parts of southern Britain.

MATERIALS AND METHODS

Clethrionomys was trapped at Salen, Isle of Mull, in May and September, 1958, and July, 1959, Clachan, Isle of Raasay, in August, 1957, Applecross, Wester Ross, in August 1957, 1958, 1959, and September, 1957, Laga, Ardnamurchan in September, 1958, and August, 1959, and Taynuilt, Argyllshire in April, 1958. Seventy-seven animals were collected from Mull, one hundred and one from Raasay and ninety-eight from the mainland. Brief reference has also been made to twenty-nine females caught at Luss, Dunbartonshire between May and September, 1956.

All animals were caught in Longworth traps. Except for a small number of trappings on Raasay each trap was set in one locality for three consecutive nights and examined daily. Trapped animals were removed and chloroformed.

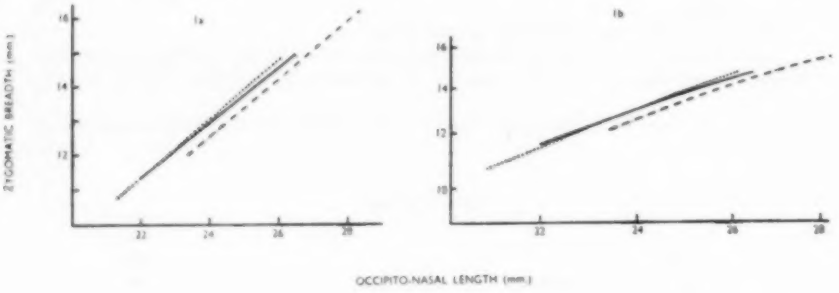


Fig. 1.—The relationship between occipito-nasal length and zygomatic breadth in skulls of *Clethrionomys glareolus* Schreb. Solid, dotted and broken lines represent *C. g. britannicus* (Miller), *C. g. alstoni* (Barrett-Hamilton and Hinton) and *C. g. erica* (Barrett-Hamilton and Hinton), respectively. The lines have been inserted between the shortest and longest occipito-nasal lengths measured in each series. (a) Linear scale. (b) Logarithmic scale.

Trapping and killing in this way prevented damage to the skull and skin which were required for further examination. All animals were weighed, to the nearest gramme, and measured, to the nearest millimetre, on the day of capture. In skinning, a small transverse incision was made immediately anterior to the external genitalia. The skin was gradually worked off the animal from the hind portion of the body forwards and the bones left in the tail and the lower portions of the limbs. The inner surface of the skin was coated with borax and the skin mounted on a stiff, shaped card. This method involved little cutting of the abdomen and displayed the belly markings satisfactorily.

Heads were removed in the field, placed in preservative (approximately 95 per cent alcohol) and examined on return to the laboratory. They were boiled in water for about an hour and the flesh then picked off them. They were then placed in hydrogen peroxide overnight and finally dried in a warm oven (57°C.). Occipito-nasal length was measured with calipers graduated

to 0·1 mm. ; zygomatic breadth was measured with a microscope possessing a graduated (to 0·1 mm.), moving stage and a micrometer eyepiece.

The length of the anterior root of the third upper molar was obtained (to 0·01 mm.) using a graduated micrometer eyepiece. The measurement was made at right angles to the grinding surface from the arch between the two roots to a point level with the extremity of the anterior root.

SKULL STRUCTURE

Small variations in skull proportions were obtained when comparing occipito-nasal length against maximum zygomatic breadth. The data for each subspecies have been analysed separately and of the mainland material only animals from Applecross were used. Regression lines have been calculated (Table 1 and Fig. 1) on linear and logarithmic scales and have been

TABLE 1

Relationship between occipito-nasal length and zygomatic breadth in *Clethrionomys glareolus* Schreb. from various localities in Scotland.

Subspecies	Locality collected	No.	Regression line (linear)	r	Regression line (logarithmic)	r
C.g. britannicus	Applecross	46	$Y=0{\cdot}786X-5{\cdot}919$	0·88	$Y=0{\cdot}136X^{1{\cdot}434}$	0·87
C.g. alstoni	Isle of Mull	60	$Y=0{\cdot}843X-7{\cdot}161$	0·90	$Y=0{\cdot}095X^{1{\cdot}548}$	0·91
C.g. erica	Isle of Raasay	39	$Y=0{\cdot}830X-7{\cdot}436$	0·96	$Y=0{\cdot}093X^{1{\cdot}543}$	0·96

compared statistically. The data fit the two types of lines closely ($r=0{\cdot}87$–$0{\cdot}96$) and in no case (Table 2) is there significant difference ($P=0{\cdot}4$–$1{\cdot}0$) between any pair of lines. The occipito-nasal length of the largest skull from Raasay was 28·2 mm., from Mull 26·1 mm. and from Applecross 26·5 mm.

TABLE 2

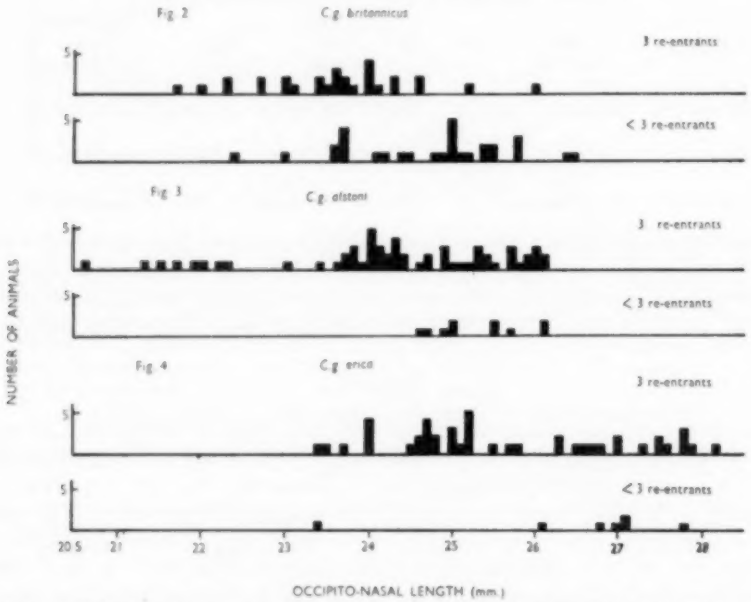
Tests of significance (P) between regression lines appearing in Table 1.

log. / linear	*C.g. britannicus*	*C.g. alstoni*	*C.g. erica*
C.g. britannicus		1–0·9	0·5–0·4
C.g. alstoni	0·5–0·4		1–0·9
C.g. erica	0·6–0·5	0·9–0·8	

Nine large mainland skulls were compared with nine of similar occipito-nasal length from both Mull and Raasay. The Mull and mainland skulls were very similar whilst those from Raasay were slightly different. The frontal and parietal bones of the latter were frequently, but not invariably, more arched and the molar teeth less worn. The angle of the lower jaw was a large, heavy structure in the Raasay material whereas in the mainland and Mull animals it showed greater variation. Occasionally, it was as large in *C. g. britannicus* as in *C. g. erica* although in most cases it was a slender structure with a deeper, larger notch between the condyle and the angle. No more

distinctive characters could be traced as skulls from one locality showed appreciable variation between one another. Thus, although the Raasay skulls attain a greater size and generally have a slightly heavier angle to the lower jaw there is no indication of consistent differences in either the general proportions or the detailed structure of the skulls of the three subspecies.

The third upper molar shows considerable structural variation. In some specimens three re-entrants (complex tooth) are clearly visible on the inner margin. In contrast, two teeth in older skulls, were devoid of re-entrants. Between the two extremes a series of intermediates were found with no clear distinction existing between the complex and simplex tooth. In examining this character the well-formed, deeply-cut re-entrant was distinguished from the incompletely eliminated one. Only the former was recorded as a complete re-entrant. On the basis of this distinction 87 per cent of the teeth from Raasay, 86 per cent from Mull and 49 per cent from Applecross showed the complex character. The number of re-entrants present in relation to skull length are given in Figs. 2–4. In *C. g. britannicus* (Fig. 2), 73 per cent of



Figs. 2–4.—Relationship between number of re-entrants on the inner margin of the third upper molar and occipito-nasal length of skull in *Clethrionomys glareolus* Schreb. Fig. 2, *C. g. britannicus* (Miller). Fig. 3, *C. g. alstoni* (Barrett-Hamilton and Hinton). Fig. 4, *C. g. erica* (Barrett-Hamilton and Hinton).

the skulls 24·0 mm. or less have molars with three re-entrants and 76 per cent of the skulls more than 24·0 mm. long have less than three re-entrants. In the Mull and Raasay voles (Figs. 3 and 4), with one exception, only the larger individuals have less than three re-entrants. Unlike *C. g. britannicus*, a higher

proportion of molars with three re-entrants are found in the larger skulls ; 79 per cent of the Mull skulls of more than 24·0 mm. length have molars with three re-entrants.

The number of re-entrants has also been compared with the age of the tooth as indicated by root-length (Table 3). It is apparent that in all three subspecies the proportion of teeth with less than three re-entrants is greater in older ones than in those more recently erupted. Comparison of the younger teeth from the three localities suggests that a higher proportion with three re-entrants appear in animals from Mull and Raasay. The Mull voles showed

TABLE 3

Relationship between number of re-entrants and length of anterior root of third upper molar in *Clethrionomys glareolus* Schreb. from various localities in Scotland.

No. of re-entrants	Length of anterior root of third upper molar (mm.)							Total
	0·00–0·29	0·30–0·59	0·60–0·89	0·90–1·19	1·20–1·49	1·50–1·79	1·80–2·09	
Mainland								
3	35	1	–	3	4	–	–	43
< 3	18	–	2	2	10	10	–	42
Mull								
3	26	–	6	12	4	3	–	51
< 3	3	–	1	6	2	3	–	15
Raasay								
3	43	–	–	–	4	13	–	60
< 3	2	–	–	–	–	4	1	7

a tooth abberration not seen in either the mainland or Raasay animals. This involved the production of a small third root between the other two. In four animals it was present in teeth from both sides whilst in eleven more it occurred in only one member of the pair. No measurements were made on teeth in the former group and only on the normal tooth in the latter.

After eruption, the molars gradually wear down and in so doing eliminate those re-entrants that do not extend down the full depth of the tooth. It is therefore possible that the frequency of the complex tooth within a population could vary in relation to the age structure of the population. This could account for the higher frequency of the complex tooth in the present series from Mull and the mainland than those collected by Steven (1953).

COAT COLOUR

Visual comparison has been made of seventeen adult skins from Raasay, thirty from Mull and forty-seven from the mainland. The fur on the back of mainland and Mull voles covered the same colour range. This varied between a light and dark chestnut-red. All the Raasay skins fitted within the range although there were a larger proportion of darker skins in this collection.

The belly fur in the mainland voles varied between a pale grey through a medium grey, pale buff, buff to medium buff. The series showed a steady increase in the intensity of the buff colouring of the fur. The Mull skins fitted within the series. Their range was more restricted as it lacked the palest and medium-dark buff individuals. The lightest Raasay voles were medium grey and at the other end of the series skins of rich dark buff contained greater depth of colour than any of the mainland skins.

Barrett-Hamilton and Hinton (1913 a, 1913 b) claimed that *C. g. alstoni* was a dark subspecies with the underside strongly tinted with buff and that *C. g. erica* had an equally dark upper surface and a more buff belly. The distinction between *C. g. alstoni* and *C. g. britannicus* has not been confirmed by the above observations. None of the skins in the Raasay collections were darker than the darkest *C. g. britannicus* and only those with a deep buff belly fur were distinctive.

LIFE HISTORY

Rowlands (1936) showed that the ratio of juvenile to adult males varied considerably with time. This resulted in large animals being preponderant during certain months and small ones in others. Thus in considering size differences, the three subspecies have been considered in relation to age structure of populations at different times of the year. Two measurements of size have been utilised ; they are the length of the anterior root of the third upper molar and weight. The former is probably the more sensitive measure of stage of development but inclusion of the latter permits comparison with the life cycle in southern Britain.

The tooth measurements (Table 4 and Fig. 5) for the mainland and Mull voles are similar and, with the Raasay voles, consistent with one another. From July to September each population has a distinctly bimodal distribution. The animals in the group to the left (Fig. 5) represent those born that year whilst those to the right are probably from the previous year. This is confirmed by comparison with the April and May histograms where young animals

TABLE 4

Lengths of anterior root of third upper molar of *Clethrionomys glareolus* Schreb. from various localities in north-west Scotland, 1957–1959.

Length (mm.)	April	May	July	August		September	
	Mainland	Mull	Mull	Mainland	Raasay	Mainland	Mull
0·00–0·29	–	–	7	41	46	12	24
0·30–0·59	–	–	–	1	–	–	–
0·60–0·89	2	7	–	–	–	–	–
0·90–1·19	4	10	7	1	–	–	1
1·20–1·49	–	1	3	10	4	3	2
1·50–1·79	1	–	2	7	17	2	4
1·80–2·09	–	–	–	–	1	–	–
Total	7	18	19	60	68	17	31

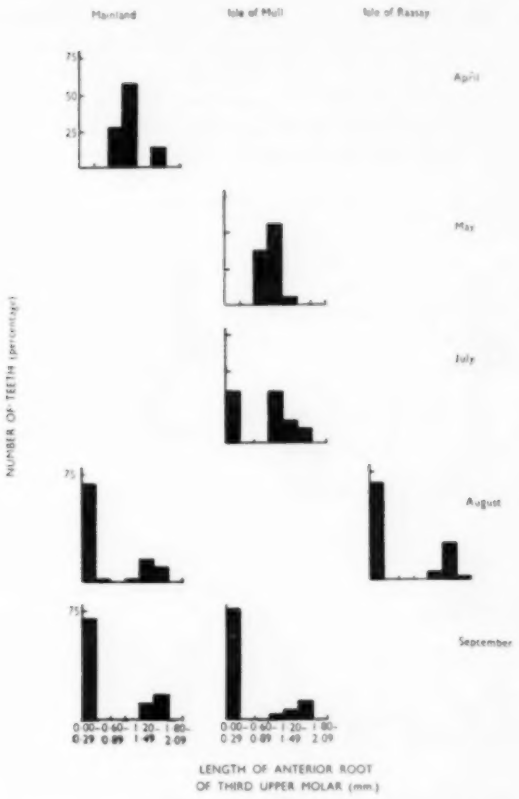


Fig. 5.—Lengths of anterior root of third upper molar of *Clethrionomys glareolus* Schreb. from various localities in north-west Scotland.

are lacking and where the main stock has not quite attained the size of the larger animals collected in July to September.

In Figs. 6 and 7 and Tables 5 and 6 the animals in each weight class are given, as available, for each month from April to September. Data obtained from north Wales and Kent by Rowlands (1936) and Brambell & Rowlands (1936) have been included. The fully grown Raasay vole is considerably larger than either the mainland or Mull vole although the distinction between the last two is ill-defined. The heaviest non-pregnant Mull vole was a male weighing 33 grammes and was trapped on September 6th, 1958 ; the heaviest mainland male was trapped at Laga on August 4th, 1959 and weighed 31 grammes. From both localities a small number of voles weighing 30 grammes have been collected in addition to two individuals from Mull weighing over 30 grammes. If size is expressed as head-and-body length then the largest record is of a female collected from Mull in September, 1958, measuring 117 mm. A male and a female from Applecross, each measuring 116 mm., were trapped in

August, 1957. The largest skull (p. 411) was obtained from a mainland vole. These differences do not establish either the mainland or Mull vole as attaining a greater maximum size and are probably of so small a magnitude as to have no significance. This is confirmed by examining Figs. 6 and 7. The weight classes into which the mainland vole falls at various times of the year are not markedly different from, nor inconsistent with, those of the Mull vole.

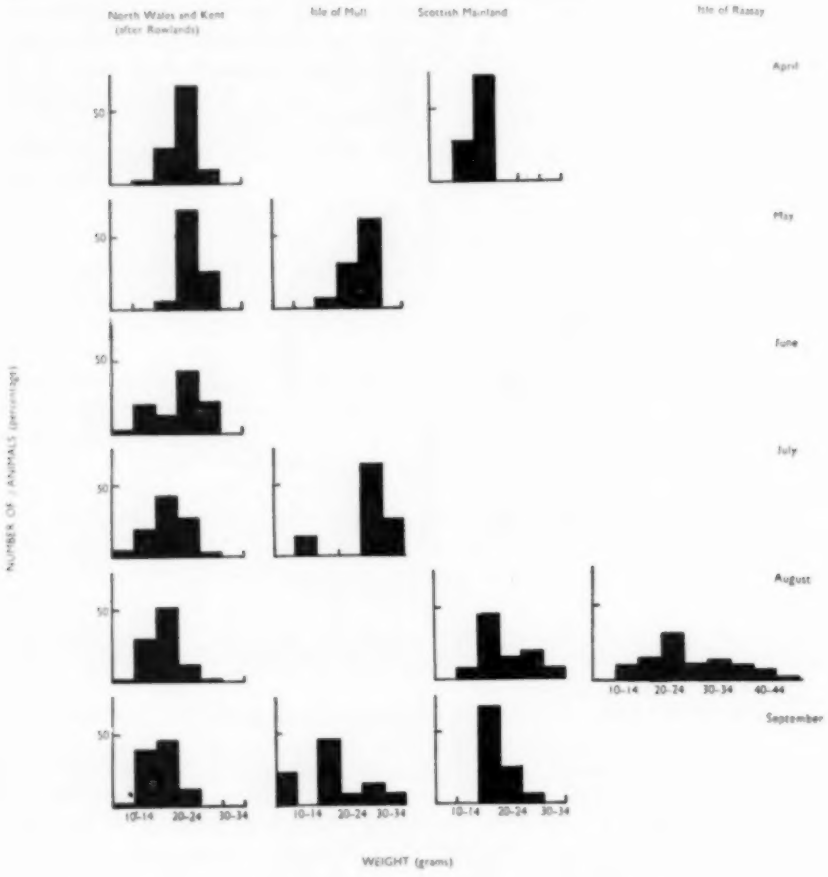


Fig. 6.—Weights of males of *Clethrionomys glareolus* Schreb. from various localities in north-west Scotland compared with weights obtained by Rowlands (1936) in north Wales and Kent.

In April and May, the population structure of male voles in north-west Scotland is not greatly dissimilar from those further south (Fig. 6) although the mainland collection for April did contain an abundance of small animals. By July, the situations are quite different. Apparently, in the south, a large number of young animals have entered the population and the majority of

the large ones have left it ; whereas on Mull few young voles are present and the large ones still comparatively numerous. It is not until August that the young animals are abundant in Scotland. The retention of a large number of animals weighing 25 grammes or more, from July to September, is in marked contrast to the situation further south. It appears that on the mainland and

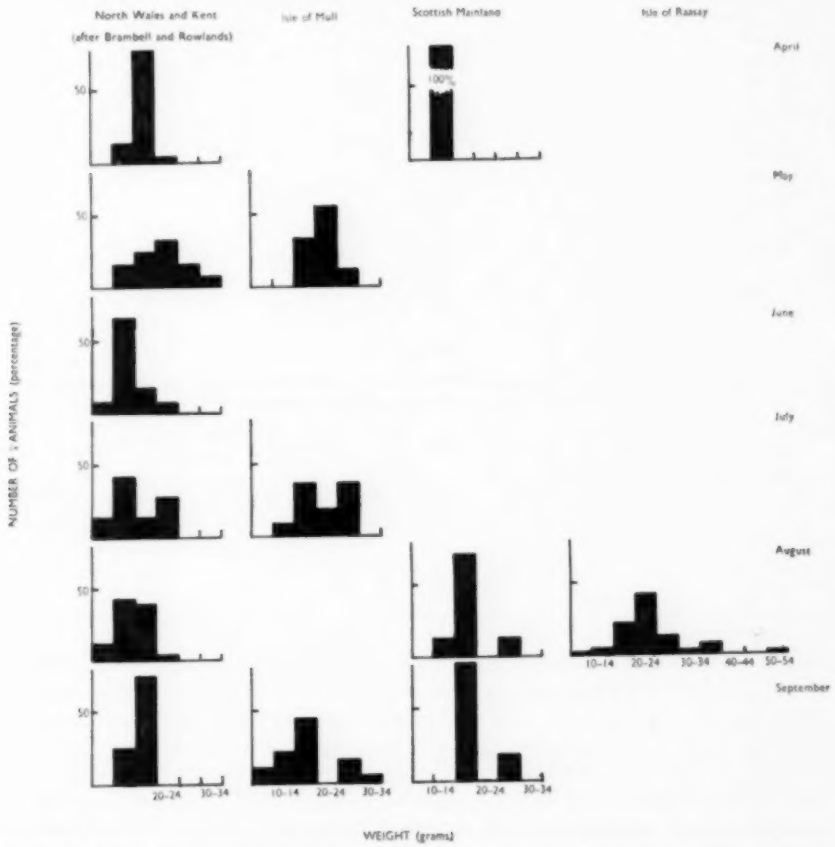


Fig. 7.—Weights of non-pregnant females of *Clethrionomys glareolus* Schreb. from various localities in north-west Scotland compared with weights obtained by Brambell & Rowlands (1936) from north Wales and Kent.

Mull, a larger proportion of the voles adult in spring survive the following summer. That the same situation prevails on Raasay is suggested from the bimodal structure of the August histograms for the island and the mainland. It is possible that the mainland and Mull males attain a slightly larger size than those from the south as some fall into a weight class (30–34 grammes) unoccupied by the latter.

The females (Fig. 7 and Table 7) show a similar life-cycle to the males except in the appearance, on Mull, of rather more young animals in July.

TABLE 5

Weights of males of *Clethrionomys glareolus* Schreb. from various localities in north-west Scotland, 1957–1959.

Weight class (grammes)	April	May	July	August		September	
	Mainland	Mull	Mull	Mainland	Raasay	Mainland	Mull
5– 9	–	–	–	–	–	–	3
10–14	2	–	1	4	6	–	–
15–19	5	1	–	21	9	8	6
20–24	–	4	–	7	18	3	1
25–29	–	10	5	9	6	1	2
30–34	–	–	2	4	7	–	1
35–39	–	–	–	–	6	–	–
40–44	–	–	–	–	4	–	–
45–49	–	–	–	–	1	–	–
50–54	–	–	–	–	–	–	–
Total	7	15	8	45	57	12	13

TABLE 6

Weights of non-pregnant females of *Clethrionomys glareolus* Schreb. from various localities in north-west Scotland, 1957–1959.

Weight class (grammes)	April	May	July	August		September	
	Mainland	Mull	Mull	Mainland	Raasay	Mainland	Mull
5– 9	–	–	–	–	1	–	2
10–14	3	–	1	3	2	–	4
15–19	–	3	4	15	9	5	8
20–24	–	5	2	–	16	–	–
25–29	–	1	4	3	5	1	3
30–34	–	–	–	–	1	–	1
35–39	–	–	–	–	3	–	–
40–44	–	–	–	–	–	–	–
45–49	–	–	–	–	–	–	–
50–44	–	–	–	–	1	–	–
Total	3	9	11	21	38	6	18

Comparison of these data with those of Brambell and Rowlands (1936) is hampered by differences in the percentages of females recorded pregnant in the two areas. The figures could have been influenced by Brambell & Rowlands (1936) recognizing, as a result of more detailed examination of the reproductive system, very early pregnancies which the present study may have overlooked. Furthermore, the authors draw attention to the unexpectedly high proportion of females with tubal stages ; this they attribute to a relatively small catch of females in the later stages of pregnancy. In Scotland, the alternative trapping method may have resulted in a different percentage of pregnant females caught. However, although there are possible inconsistencies in the two sets of data it is unlikely that they would be of sufficient magnitude to radically alter the main conclusions to be drawn from

TABLE 7

The pregnant females of *Clethrionomys glareolus* Schreb. from various localities in north-west Scotland, 1956–1959.

Date	Locality	Total females	No. embryos/ female	Percentage pregnant	Percentage pregnant over month	Percentage pregnant in North Wales and Kent (Brambell & Rowlands, 1936)
APRIL						
22–30, 1958	Taynuilt	3	–	–	–	43
MAY						
5–14, 1958	Mull	8	–	–	21	84
25–27, 1956	Luss	11	4·25	36		
JUNE						
4– 6, 1956	Luss	8	3·57	88	88	62
JULY						
2– 9, 1959	Mull	13	4·00	15	12	76
15–17, 1956	Luss	4	–	–		
AUGUST						
2– 5, 1959	Laga	2	–	–		
6–23, 1957	Raasay	44	3·80	14		
7–13, 1958	Applecross	9	4·00	11	13	53
8–14, 1959	Applecross	3	–	–		
25–31, 1957	Applecross	10	4·00	20		
SEPTEMBER						
1– 5, 1957	Applecross	3	–	–		
2– 8, 1958	Mull	19	4·00	5	3	20
9–12, 1958	Laga	3	–	–		
18–20, 1956	Luss	6	–	–		

Table 7. It appears that breeding starts, in Scotland, in mid-May, reaches a peak in June and thereafter declines rather abruptly. The small catch of young animals in early July is a reflection of this comparatively late start to breeding. Further south, breeding starts earlier and reaches a peak in May. This permits a second peak to be attained in July due to the main stock attaining maturity by mid-summer. From April to September, except June, a considerably higher proportion of the females are pregnant in north Wales and Kent.

The Scottish voles do not appear to compensate for the lower incidence of pregnancy by higher litter size. The average number of embryos in a pregnant female was 4·00, 3·86 and 3·80 for Mull, the mainland and Raasay, respectively. The overall average was 3·86, a figure intermediate between the 3·82 found by Baker (1930) and the 4·11 by Brambell & Rowlands (1936). These authors found litter size to decline from July onwards and attributed it to the small, recently-matured females producing small litters. In Scotland, from the limited data available, there appears little evidence of litter size declining. As breeding starts later in the north, it would be expected that fewer females would be available to breed in the same year as they were born.

According to Brambell & Rowlands (1936) females weighing less than 20 grammes had an average litter size of 3·8, those weighing 20–24·9 grammes 4·2 and those weighing more than 25 grammes, 4·5. All the pregnant females caught in Scotland in August and September weighed at least 22 grammes. Examination of root lengths in females breeding from July to September (Table 8) suggests that during this period a large amount of breeding is carried out by animals born the previous year. Of the eighteen pregnant or lactating females examined only four were of the present year's stock.

TABLE 8

Lengths of anterior root of third upper molar in breeding females of *Clethrionomys glareolus* Schreb. from various localities in north-west Scotland, 1957–1959.

Month	Locality	Condition of females	Length of M^3 root (mm.)	No. measured
July	Mull	Lactating	1·05–1·12	2
	Mull	Pregnant	1·12–1·15	2
August	Raasay	Lactating	0·00	2
	Raasay	Pregnant	1·40–1·73	4
	Mainland	Lactating	1·58	1
	Mainland	Pregnant	0·00–1·50	3
September	Mull	Lactating	1·48–1·71	4

From the foregoing, there appears to be little justification for separating on the basis of size, the Mull and mainland voles from each other and from those collected further south. The life cycles of the Scottish mainland and island voles are consistent with one another and apparently different from those in southern Britain.

DISCUSSION

It is suggested that the differences between the Scottish subspecies of *Clethrionomys* are small. The Mull vole differs from the mainland vole only on small and variable tooth characters. The original description of *C. g. alstoni* was based on a small number of animals and no comparison was made with animals collected from the adjoining mainland at the same time of year. It has been shown that an artificial estimate of size can result from divorcing size from life history. Steven (1957) stresses the importance of size in separating Mull from mainland voles. Referring to the weight of *C. g. britannicus* he states, " . . . rarely as much as 20 g. : average 17 g." and of *C. g. alstoni*, " . . . usually more than 20 g. : average about 30 g.". Rowlands (1936) found 65 per cent to 94 per cent of the males of *C. g. britannicus* weighed more than 20 grammes between April and June. In the present study, males from the mainland of more than 20 grammes were not rare. Furthermore, only three of the seventy-four males and non-pregnant females collected from Mull weighed more than 30 grammes. The suggestion that *C. g. alstoni* has an ' average ' weight of 30 grammes is not supported by the present data. Nor is the inference that it approaches twice the weight of *C. g. britannicus*.

C. g. erica is clearly larger than both *C. g. britannicus* and *C. g. alstoni*. Reference to the skull suggests that morphological differences, e.g. more robust

zygoma, are mainly the result of increased size. The relatively small difference between the three subspecies is confirmed by Steven's (1953) ability to obtain crosses between them. It thus appears that the difference between Mull and mainland voles is insufficient to give the former even subspecific status.

Hinton (1926) suggested that the large Mull and Raasay voles were isolated relict forms of the *nageri* group which originally occurred over all Britain and which had been displaced from the mainland by a member of the smaller *glareolus* stock. The present study and the breeding experiments of Steven (1953) do not indicate the differences between mainland and island voles to be as distinct as Hinton (1926) supposed. The Mull and mainland vole are apparently of the same stock and the Raasay vole could have differentiated from this stock, as proposed by Steven (1953), in its present situation. There is a tendency for rodents to attain large size on small islands, e.g. *Apodemus* on St. Kilda (Boyd, 1959), Fair Isle (Kikkawa, 1959) and Mingulay and Berneray (Warwick, 1940) and *Microtus* in the Orkneys (Zimmerman, 1959), and it is suggested that the large *Clethrionomys* on Raasay has followed the same trend.

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SUMMARY

1. Seventy-seven specimens of *Clethrionomys glareolus alstoni*, one hundred and one of *C. g. erica* and ninety-eight of *C. g. britannicus* were collected from north-west Scotland in the summers of 1957 to 1959 as well as in the spring of 1958. The three subspecies have been compared for systematic differences and their life cycles considered in relation to each other and that of *C. g. britannicus* further south.

2. The skull proportions are similar for the three subspecies. The Raasay vole possesses a heavy angle to the lower jaw ; this occurs infrequently in *C. g. britannicus*. The three subspecies may have complex, third upper molars when young although their frequency is lower in *C. g. britannicus* ; as the tooth wears the third re-entrant is frequently eliminated.

3. The subspecies cannot be separated on coat colour except for a small percentage of Raasay voles with a deep buff belly fur.

4. Whilst *C. g. erica* is distinctly large, there is no adequate evidence of size difference between the two other subspecies.

5. The life cycles of the Scottish subspecies are consistent with each other. Breeding starts in mid-May, reaches a peak in June and then declines

abruptly. Further south, *C. g. britannicus* breeds earlier and maintains a higher level throughout the summer. In Scotland, comparatively few animals breed in the same year as they are born.

6. It is suggested that *C. g. alstoni* should not be ranked as a subspecies distinct from *C. g. britannicus* and that *C. g. erica* has evolved on Raasay from *C. glareolus* stock.

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SOME NOTES ON THE BREEDING CYCLE OF THE SENEGAL GALAGO *GALAGO SENEGALENSIS SENEGALENSIS* IN THE SUDAN

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(With 3 plates)

The Senegal galago appears to have an oestrous cycle lasting four to six weeks and recurring throughout the year. It most probably exhibits a post-partum oestrus. The intensity of sexual activity varies during the year and this gives the appearance of one or more restricted breeding periods. In the Nuba mountains there is a period of intense sexual activity in mid-December. A well-developed sequence of changes occurs in the vaginal epithelium during the oestrous cycle. These changes are typical of those seen in other mammals. The corpus luteum of pregnancy, which may become pedunculated, only lasts for about the first third of pregnancy. Twin pregnancies are uncommon.

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INTRODUCTION

A previous note (Butler, 1957) suggested that, in the Nuba Mountains, Kordofan Province, Sudan, the Senegal galago appears to have a restricted breeding season. Breeding commences in December and, with pregnancy lasting four months (Lowther, 1940), births are to be expected around March/April of the following year. There could be a second pregnancy between May and November but the seasonal rains prevent field collections during this period. Some doubt was cast on Lowther's (1940) suggestion that oestrus occurs, on an average, once in six weeks throughout the year.

MATERIAL EXAMINED

The following remarks are based upon the examination of twenty-two uteri and ovaries of the Senegal galago collected in the Nuba Mountains, a circumscribed area situated some 12° North of the Equator. The specimens

were collected in the months of December, January and March of the years 1956, 1957 and 1958. Fifteen of the twenty-two specimens were collected between the 7th and 17th of December in 1957 and 1958. In eleven specimens one or both ovaries were completely " serially sectioned ". The uterus and vagina were sectioned in selected specimens.

CYCLIC CHANGES IN OVARY, UTERUS AND VAGINA

Two specimens (Nos. 1 and 2) were taken on 28th March and 13th December 1956, respectively. Neither specimen contains corpora lutea. An assessment of follicular growth was made by counting and classifying follicles of 200 μ or more in diameter. This minimum size was chosen because preliminary examinations of various ovaries indicated that follicles of 200 μ and more have a fully grown ovum (70 μ or more in diameter) and that they are on the verge of antrum formation. These follicles can be divided into four types :

Type I. Solid follicles with no antrum formation.

Type II. A few small, but discrete, antra.

Type III. The antra are larger and either beginning to coalesce or have coalesced to form a single large antrum. In addition to a coarse eosinophilic coagulum of follicular fluid these follicles contain basophilic bodies. This is a sign of early degeneration (Pl. 1, fig. 1).

Type IV. Follicles of the same structure as Type III, but with a fine eosinophilic coagulum and no basophilic droplets. These are normal follicles (Pl. 1, fig. 2).

TABLE 1

Distribution and size range of follicles over 200 μ in diameter.

Type of follicle	Diameter of follicles μ	Number of follicles No. 1 28th March	No. 2 13th Dec.	No. 3 8th Dec.
I	200–400	22	28	13
II	300–400	3	8	1
III	200–400	10	10	2
IV	300–700	6	6	6
		41	52	22

In each specimen the uterine cornua are equal and measure 2·5 mm. in diameter and 4·0 to 4·5 mm. in length. Sections reveal, however, noticeable differences in the endometrium. In specimen No. 1 the endometrium is up to 400 μ in thickness, whereas, in specimen No. 2 it reaches a thickness of 500 μ in places. The glands are better developed in specimen 2 (Pl. 2, fig. 9) than in specimen 1 (Pl. 2, fig. 7). Noteworthy is the cellular, sub-epithelial zone which is about the same thickness in both specimens (between 50 and 100 μ). Neither specimen shows evidence of secretion.

Sections of the vagina reveal striking differences in the epithelium with a stratum granulosum and minimal cornification and is typical of the pro-oestrous stage of the oestrous cycle (Eckstein & Zuckerman, 1956). Intra-epithelial cysts containing a desquamated cell are not plentiful. On the other hand, specimen No. 2 shows massive cornification and desquamation and there are many intra-epithelial cysts. This is typical of the oestrous phase of the cycle and it is to be noted that there was an interval of $8\frac{1}{2}$ months between the dates of capture of these two specimens.

Specimen No. 3, captured on 8th December 1958, has a sub-surface corpus luteum, in the left ovary (Pl. 1, figs. 5 and 6) which measures $600 \times 500\,\mu$. A small remnant of the follicular cavity is seen but there is no haemorrhage into it. Serial sections of the left uterine tube and cornu failed to reveal the discharged ovum.

An analysis of follicles over $200\,\mu$ in diameter is given in Table 1. There is a very considerable reduction in the total number of follicles. This is partly due to there being less follicles without either antra or early antrum formation and partly, because Type III follicles are now in a more advanced stage of degeneration and so are not included in the counts. The Type IV follicles are now much larger, some being from 600 to $700\,\mu$ in diameter and, as is to be expected, the early corpus luteum is about this size. A typical example of a large follicle is shown in Pl. 1, fig 3 and it is to be noted that the cumulus oöphorus now has a slender stalk and no antra (compare with fig. 2). This picture of follicular development, which is more advanced than that of the other specimens, can be regarded as typical of pre-ovulatory follicles.

The uterine horns are of equal size and measure 3·0 mm. in diameter and 6·0 mm. in length. The endometrium (up to $600\,\mu$) and, in particular, the sub-epithelial zone are thicker and more densely packed with cells (Pl. 2, fig. 11). The uterine lumen contains a basophilic secretion, numerous leucocytes and some extravasated blood. The uterine epithelium is, however, intact (Pl. 3, fig. 13). There is no cornification of the vaginal epithelium but a massive invasion by leucocytes (Pl. 2, fig. 12).

A further specimen, taken on 10th December 1957, has a corpus luteum in each ovary. Each measures over 1·0 mm. in diameter and bulges above the surface of the ovary. Sections of the left uterine tube revealed a degenerating tubal ovum. The endometrium shows more advanced progestational changes but, in both uterus and vagina, the leucocytic invasion has subsided. There is no cornification of the vaginal epithelium.

DISTRIBUTION OF PREGNANCIES

Table 2 shows the temporal sequence of the eleven specimens in which the stage of pregnancy has been ascertained, together with two records of live births. Seven other pregnant specimens, obtained between 8th and 17th December in 1957 and 1958, have not yet been serially sectioned. Nevertheless, the state of development of the uterine cornua and the corpora lutea indicate that all contain either tubal ova or blastocysts. The raucous mating

call of the female is heard all night long at this period of the year (Watson-Baker, 1956). Blastocysts A, B, C have maximum diameters of 4·0, 4·5 and 5·5 mm. respectively.

TABLE 2

Date of capture	State of pregnancy
11th December, 1957	Blastocyst A
17th December, 1957	Blastocyst B
17*th December*, 1957	*Blastocyst C*
29th December, 1957	4·0 mm. C.R. length embryo
10th January, 1956	12·6 mm. C.R. length embryo
14th January, 1956	12·0 mm. C.R. length embryo
21*st January*, 1958	*Blastocyst C*
24th January, 1958	20·0 mm. C.R. length embryo (two specimens)
7th March, 1957	40·0 mm. C.R. length foetus
19th March, 1959	Live birth
28th March, 1956	54·0 mm. C.R. length foetus
1st June, 1958	Live birth

The 54·0 mm. C. R. length foetus has open eyes and a well-developed pelage and is, therefore, regarded as being very near to term. The animal which gave birth on 19th March, 1959, was collected on 17th December, 1958, i.e. the period when early pregnancies are abundant. It was not in contact with an adult male after its capture thus, pregnancy lasted at least three months. Immediately after birth the mother emitted the raucous mating call. Oakley (1959) observed the same phenomenon following a still-birth on 27th June, 1959. Hill (1957) records the occurrence of a live birth on 1st March, 1946. Both the latter two births occurred in captivity in London. Note that the two specimens of blastocyst C are separated by an interval of five weeks.

THE CORPUS LUTEUM OF PREGNANCY

The corpus luteum of pregnancy is, at first, subsurface but as it grows it bulges more and more out of the ovary and may become completely pedunculated (Pl. 3, fig. 14). It attains a maximum diameter of 1·5 to 2·0 mm. during early pregnancy. By the time the embryo is 4·0 mm. C.R. length the corpus luteum of pregnancy is reduced to 1·0 mm. in diameter. When the embryo is some 12·0 mm. C.R. length the corpus luteum of pregnancy has been replaced by a corpus albicans which is only 0·5 mm. in diameter and completely devoid of luteal cells (Pl. 3, figs. 15 and 16). The corpus albicans is still clearly visible when the embryo is 20·0 mm. C.R. length. None of the ovaries examined show any indication of the formation of accessory corpora lutea during pregnancy.

POST-PARTUM OESTRUS

With one exception the ovaries of the later pregnancies show degenerating follicles of all sizes, primoridal follicles and follicles in the first growth phase, i.e. with an ovum measuring 60 μ or less in diameter and with only four to six layers of follicle cells. No antra are found in these young follicles. The

ovary of the mother of the near term foetus contains several large follicles in the second growth phase, i.e. 200 to 500 μ in diameter and with late antrum formation (Pl. 1, fig 4). Their contained ova measure 75 to 80 μ in diameter. They are indistinguishable from the growing follicles in the ovaries of the mature, non-pregnant animals taken in December and March.

As pregnancy advances the vaginal epithelium becomes reduced in thickness and may even become only one cell thick (Pl. 3, fig. 17). However, the vagina of the mother with the near term foetus (C.R. 54·0 mm.) shows a return to several layers of cells (Pl. 3, fig. 18). The significance of the desquamating layer of cells is not yet clear but the renewed growth of the epithelium is in keeping with the return of follicular activity.

DISCUSSION

Specimens Nos. 1, 2 and 3 clearly demonstrate the pre- and post-ovulatory changes in the ovary, uterus and vagina in the Senegal galago. On the evidence from the ovary alone it was not possible to be certain of the relative stage of the oestrous cycle in specimens Nos. 1 and 2. The general picture of follicle growth was very similar in both, although specimen No. 2 had a greater total number of large follicles. Sections of the endometrium, however, indicated that specimen No. 2 was in a somewhat later stage than specimen No. 1. Their position in the cycle was clearly indicated by the structure of the vaginal epithelium ; that of specimen No. 1 being typical of pro-oestrus and specimen No. 2 of oestrus. Specimen No. 2, although in the oestrous phase, had not reached the stage of the pre-ovulatory swelling, since the largest follicles are no more than 500 μ in diameter, whereas, the largest unruptured follicles in the post-ovulation specimen are between 600 and 700 μ in diameter.

The post-ovulation specimen (No. 3) has an early corpus luteum which is just slightly less in diameter than the largest unruptured follicle. In this specimen ovulation was not accompanied by haemorrhage into the follicle. The thicker endometrium has a dense sub-epithelial zone containing many leucocytes. The lumen of the uterus contains basophilic secretion, many leucocytes and some extravated blood. The endometrium is intact and there is no evidence of loss of uterine epithelium as was described in *Loris* by Naryan Rao (1932). There is no cornification of the vaginal epithelium but there is a massive leucocytic invasion. As the corpus luteum increases in size the leucocytes disappear.

Although the material is scanty these specimens clearly indicate that the reproductive organs of the Senegal galago undergo cyclic changes typical of the oestrous cycle of other mammals. Cyclic changes in the vaginal epithelium have not previously been described in any Strepsirhine although Hill (1953) observed the shedding of a complete hollow cast of the vaginal cavity in a recently delivered *Loris*.

The pro-oestrous specimen was taken in March and the oestrous and post ovulation specimens in December. The long time interval between them (8½ months) suggests that these are phases of two separate cycles and not of the same cycle. This is confirmed by the finding of two blastocysts of the same age group C, separated by an interval of five weeks. Oakley (1959)

observed mating activity in a pair of captive galagos (in London) during the second week in December 1958, and in the second week of January 1959. In the second week of February 1959 there were slight indications of mating activity, but the female did not exhibit the characteristic call, much in evidence in December and January. A single off-spring was still-born on 27th June, 1959. It is further to be noted that the recorded births, in Kordofan, occurred on 19th March and 1st June and a near-term foetus was found on 28th March. This evidence accords with Lowther's (1940) observations that the Moholi galago (the southern equivalent of the Senegal galago) exhibits oestrus at four- to six-week intervals throughout the year.

The earlier evidence presented (Butler, 1959) suggested a restricted breeding period, in Kordofan, commencing in December and with births in March/April. It is now clear that, while there is intense reproductive activity in mid-December when all mature specimens show oestrus, ovulation or early pregnancy, reproduction can occur at other times. This is clearly indicated by the temporal spacing of the specimens of blastocysts of the age group C and the spread of births. Thus, it is most probable that the Senegal galago is polyoestrous and, because of variations in breeding intensity, there appears to be at least one restricted breeding season. This would also seem to apply to the Moholi galago since Lowther's (1940) observations indicate a polyoestrous cycle but the evidence from birth records (Zuckerman, 1952) indicates peaks in April/May and October. Such seasonal variations imposed on a polyoestrous cycle are seen in several mammals, e.g. Sciuridae (Asdell, 1946). Unfortunately, it is not possible to collect in the Nuba Mountains between May and November because of the rains but it is quite possible that the Senegal galago shows a second peak of reproductive activity during this period. Male animals collected in the Nuba Mountains in December and March show active spermatogenesis. Little is known about other Strepsirhine (Hill, 1953), but the available evidence suggests that *Lemur* and *Loris* have an annual or bi-annual breeding cycle with a long intervening phase.

Follicular growth, comparable to that seen in the pro-oestrous specimen, is seen in the ovary of the mother with the near term foetus. This is associated with growth of the vaginal epithelium and the mother emits the characteristic mating call after birth (Oakley, 1959). These facts may be regarded as strong presumptive evidence that the Senegal galago exhibits a post-partum oestrus.

Lowther (1940) found that pregnancy lasted for four months in the Moholi galago in captivity and the evidence presented in Table 2 indicates that this is probably true also for the Senegal galago in the Nuba Mountains.

In the Senegal galago the corpus luteum of pregnancy is transformed into a corpus albicans by the time the embryo is some 12·0 mm. C.R. length and the available evidence suggests that this occurs about one third of the way through pregnancy. There is no evidence of further formation of corpora lutea and it is to be presumed that the placenta takes over the function of maintaining pregnancy.

It is often stated that twin pregnancies are very common in the Galagidae. Out of a total of twenty-two records of either ovulation, pregnancy or live

births there are only two instances of twinning. Haddow (1956) has examined many pregnant specimens of *G. s. senegalensis*, *G. crassicandatus* and *Galagoides demidovii* but has rarely encountered twins.

ACKNOWLEDGMENTS

I wish to record my thanks to Dr Mohamed Zaki Mustafa and Dr Ali Mohamed Nur for their invaluable help in collecting this material ; also to Mrs Wendy Husband for looking after the live animals and recording the births and, finally to Mr S. J. Woods for preparing the histological sections.

ADDENDUM

Since writing this paper a further seven uteri were collected between the 28th and 30th of December, 1959. Six are in varying stages of early pregnancy and one specimen contains a tubal ovum with the male and female pronuclei about to fuse. The vagina of this specimen is over twice the size of any previously seen. It is lined by stratified squamous epithelium, some 400 μ thick, with massive cornification and this is regarded as the condition reached at ovulation. The largest blastocyst measures some 10·0 mm. in diameter. The non-pregnant specimen is in a later stage of follicular growth than either of the specimens Nos. 1 and 2 described above.

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EXPLANATION OF PLATES

Plate 1

Fig. 1.—Type III follicle showing basophilic droplets in the follicular fluid. Early degeneration during proestrus.

„ 2.—Type IV follicle without basophilic droplets. A normal growing follicle of the proestrous phase.

Fig. 3.—A large unruptured follicle form specimen No. 3 (early post-ovulatory phase). This illustrates the size and structure of the Graafian follicle just prior to ovulation.

„ 4.—A moderately large growing follicle from the ovary of the mother bearing a near term foetus. Compare with Fig. 2.

„ 5.—The early corpus luteum of specimen No. 3. Compare its size with that of the follicle in Fig. 3.

„ 6.—Part of the corpus luteum shown in Fig. 5 at a higher magnification. Note remnant of follicular cavity and absence of haemorrhage.

PLATE 2

Fig. 7.—Section of the endometrium of specimen No. 1. Pro-oestrous phase.

„ 8.—Section of the vaginal epithelium of specimen No. 1. Pro-oestrous phase. Note minimal cornification.

„ 9.—Section of the endometrium of specimen No. 2. Early oestrous phase. Glands are more prominent.

„ 10.—Section of the vaginal epithelium of specimen No. 2. Early oestrus. Note massive cornification and desquamation.

„ 11.—Section of the endometrium of specimen No. 3. Early post-ovulatory phase.

„ 12.—Section of the vaginal epithelium of specimen No. 3. Early post-ovulatory phase. Massive leucocytic invasion.

PLATE 3

Fig. 13.—High power view of uterine epithelium and uterine cavity to show leucocytes and extravasated blood in the post-ovulatory phase. Specimen No. 3.

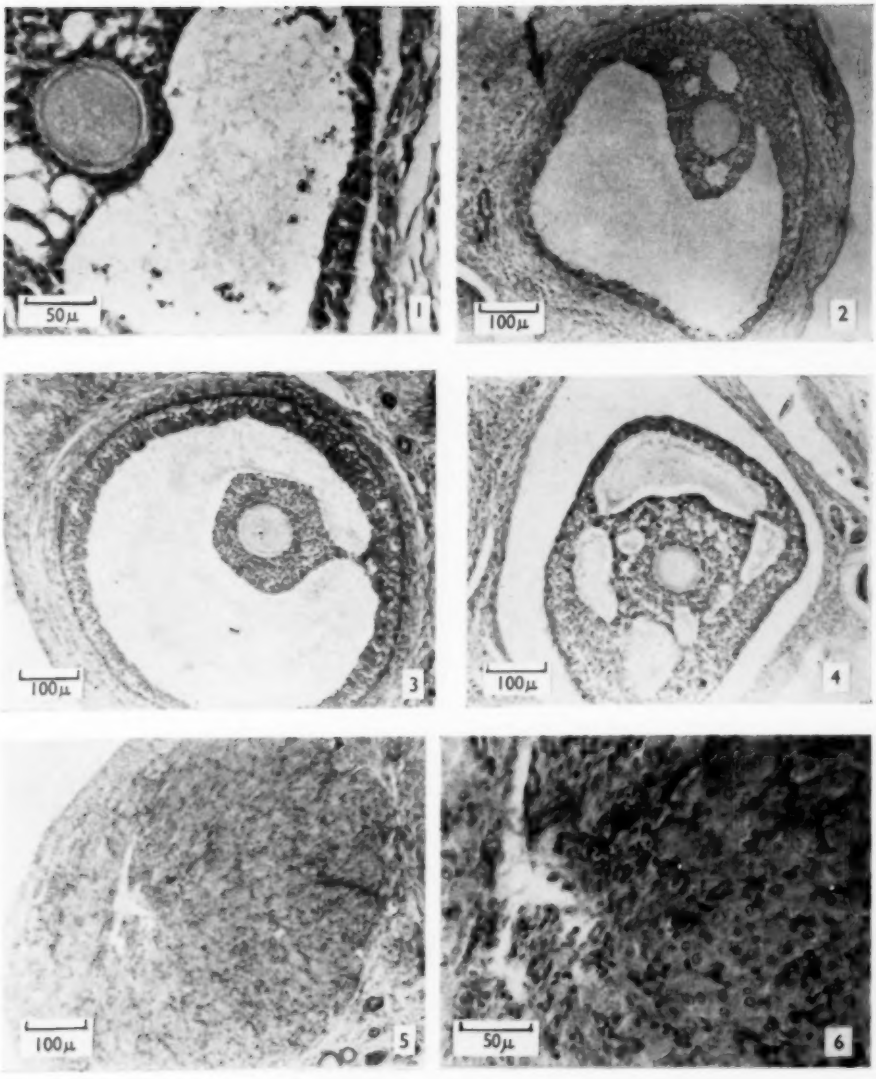
„ 14.—Pedunculated corpus luteum of pregnancy ; from a specimen containing a blastocyst C.

„ 15.—Low power view of the corpus albicans. Uterus contained a 12·0 mm. C.R. length embryo.

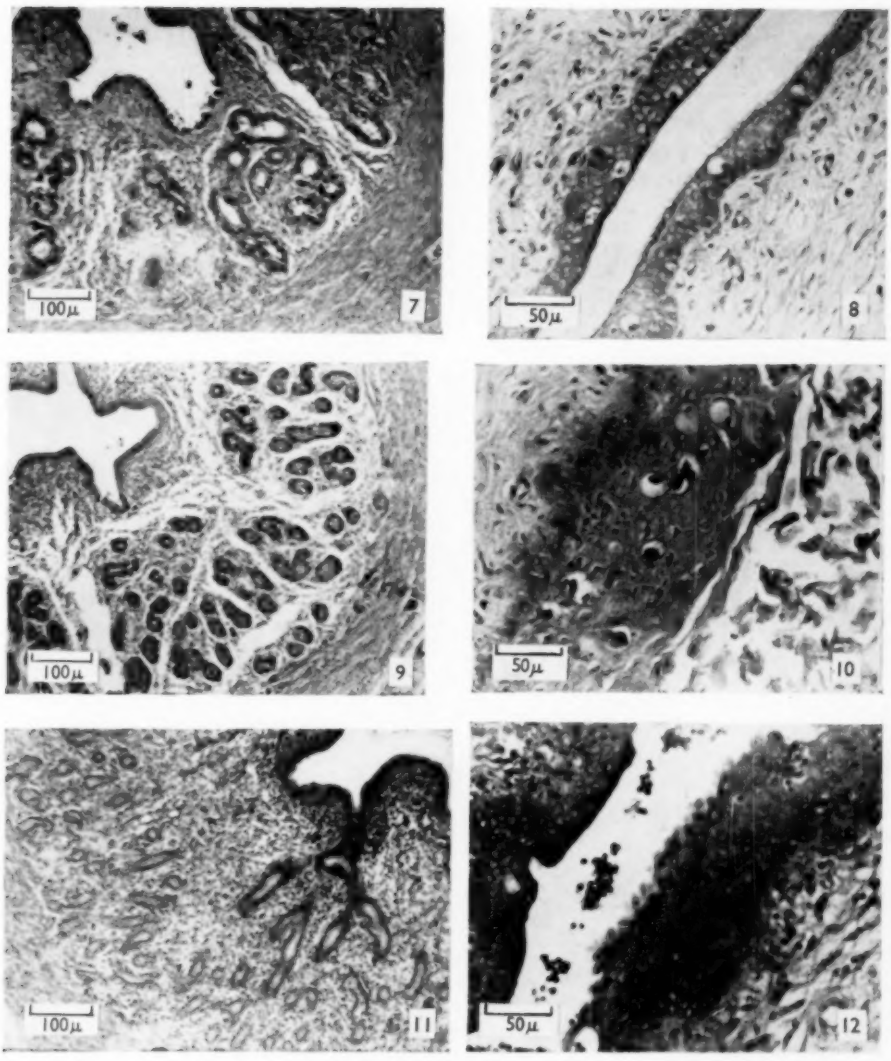
„ 16.—High power view of corpus albicans to show complete absence of luteal cells.

„ 17.—Section of the vaginal epithelium during pregnancy. Uterus contains a blastocyst C.

„ 18.—Section of the vaginal epithelium of the mother bearing the near-term foetus. A growing follicle from the same ovary is shown in Fig. 4.



The breeding cycle of the Senegal galago.



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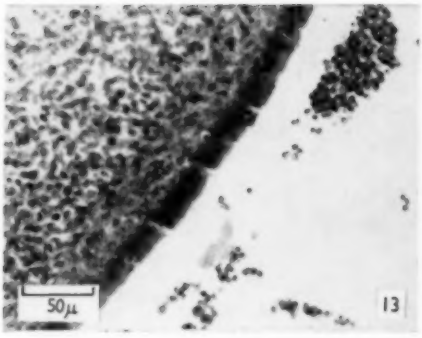

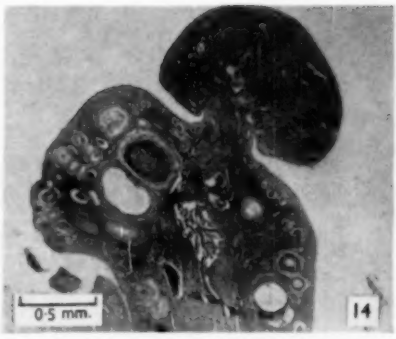

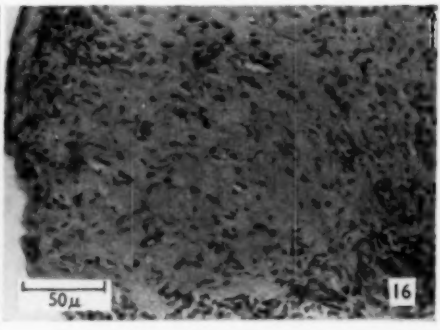

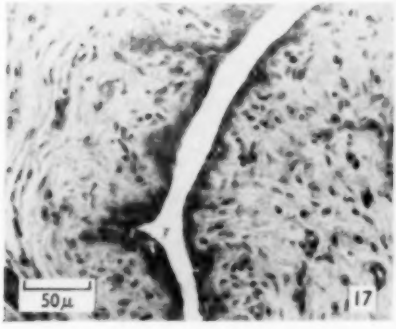

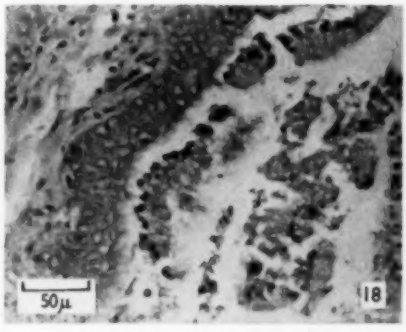

The breeding cycle of the Senegal galago.

THE STOMACH IN THE EULAMELLIBRANCHIA; STOMACH TYPES IV AND V

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(With 19 figures in the text)

The internal structure and function of the stomach is described for representatives of twenty-three families of Eulamellibranchia. The stomachs of two of these are assigned to Stomach Type IV and the remainder to Stomach Type V. A detailed analysis is made of structural variation in the stomach in the twenty-one families with stomachs of Type V and a definition of Stomach Type V is given. The appendix is limited in its occurrence to the Tellinacea and the Adesmacea, which suggests that these two sub-orders are closely related to each other. It is concluded that Stomach Type IV is an ancestral character which has persisted to the present time in a large section of the Lamellibranchia; it is suggested that there arose from the ancestral stock a separate phylogeny which is characterized by the possession of Stomach Type V. It is concluded that within the phylogeny that is chara teri ed by Stomach Type V it is possible for the stomach to be simplified and to resume secondarily the ancestral form of Stomach Type IV. This is considered to have occurred in the Sphaeriidae, Lucinidae, Thyasiridae, Donacidae and in *Chama multisquamosa*.

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INTRODUCTION

In previous papers (Purchon, 1957, 1958) the structure and function of the stomach was described for four families in the Filibranchia and Pseudolamellibranchia, and for seventeen families in the Eulamellibranchia in which the stomach was of Type IV. The brief description of the interior of the stomach of *Brechites penis* given in the second of these papers was derived from study of a preserved specimen. A second living specimen of this very rare species has been obtained and the opportunity taken to make a thorough study of its stomach, on the basis of which a more detailed account and an illustration are provided in the present paper. In addition an illustrated

account is given of the stomach of *Donax faba*, which was surprisingly found to have a stomach of Type IV. This raises the total number of families known to have a stomach of Type IV to twenty-two.

The greater part of the present paper is devoted to a survey of twenty-one families in the Eulamellibranchia which in contrast possess a stomach of Type V. All the material studied was living, with exception of *Corbicula japonica* of which preserved specimens were kindly supplied and identified by Dr A. Fuji, Faculty of Fisheries, Hokkaido University, Hakodate, Japan. Specimens of *Dreissena polymorpha* were kindly supplied by Dr E. Windle Taylor, Director of Water Examination, Metropolitan Water Board, London ; specimens of *Dosinia lupinus* were supplied by the Director of the Laboratory, Citadel Hill, Plymouth. The work on *Dreissena*, *Cyprina*, *Dosinia* and *Mya* was carried out at the Department of Zoology, University of Bristol, through the courtesy of Professor J. E. Harris, F.R.S. Study of *Gafrarium*, *Lucinopsis*, and *Aloidis* was carried out at Millport in September 1955 while the writer was the recipient of financial aid from the Browne Research Fund of the Royal Society. The remainder of the material was studied at the Department of Zoology, University of Malaya, Singapore. Specimens of *Donax faba*, *Geloina ceylanica*, *Chama lazarus*, *Trapezium sublaevigatum* *Mactra mera*, *Atactodea glabrata*, *Caecella cumingiana*, *Tellina capsoides*, *Gari togata*, *Asaphis deflorata*, *Pharella acuminata*, and *Glaucomya* (=*Glauconome*) *rugosa* were kindly identified by Professor R. Tucker Abbott, Academy of Natural Sciences, Philadelphia. Specimens of *Dosinia lupinus* were identified by Dr D. Atkins, Dr D. B. Carlisle and Dr G. M. Spooner at the Laboratory, Citadel Hill, Plymouth. Specimens of *Teredo manni* and of *Psiloteredo amboinensis* were identified by Miss Ruth D. Turner, Museum of Comparative Zoology, Harvard College. The writer wishes to acknowledge with thanks the valuable help given by the Royal Society, the Directors and Staff of the Marine Biological Stations at Plymouth and at Millport, and all the persons mentioned above.

STOMACH TYPE IV

Representatives of twenty-one families of bivalves possessing a stomach of this type have been described (Purchon, 1957 ; 1958). In the present paper an illustration and a more detailed account is given of one of these, namely *Brechites penis* (p. 433). An illustration and a description is also given of the stomach of *Donax faba* (p. 435), a representative of an additional family, so that in all twenty-two families are now known to possess stomachs of Type IV. These additional data do not conflict with the definition of Stomach Type IV as amended (Purchon, 1958), though the Donacidae should be added to the exceptions listed in paragraphs 2 (mid-gut separate from the style-sac), 4 (no distinct sorting area in the dorsal hood), 5 (the minor typhlosole is absent), 6 (the major typhlosole and intestinal groove pass deeply into a cavity on the left anterior floor of the stomach). The Clavagellidae should be added to the exceptions listed in paragraph 7 (no ducts enter the left pouch), while in paragraph 8 the Clavagellidae form an additional example in which the food-sorting caecum and sorting areas are somewhat reduced.

Description of Material

CLAVAGELLACEA

Clavagellidae

Brechites penis (L.) (Fig. 1)

The digestive diverticula form a compact yellowish green mass which lies on the anterior side of the stomach and extends far downwards into the visceral mass. The diverticula cannot be teased apart ; when ruptured they exuded what appeared to be small oil globules from the broken surfaces. The oesophagus (O) enters the stomach by a wide circular orifice with slightly raised lips. A ridge (R) passes backwards from the right margin of the oesophageal orifice, over the roof of the stomach and into the dorsal hood (DH), and ciliary currents on either side of this ridge carry particles into the dorsal hood.

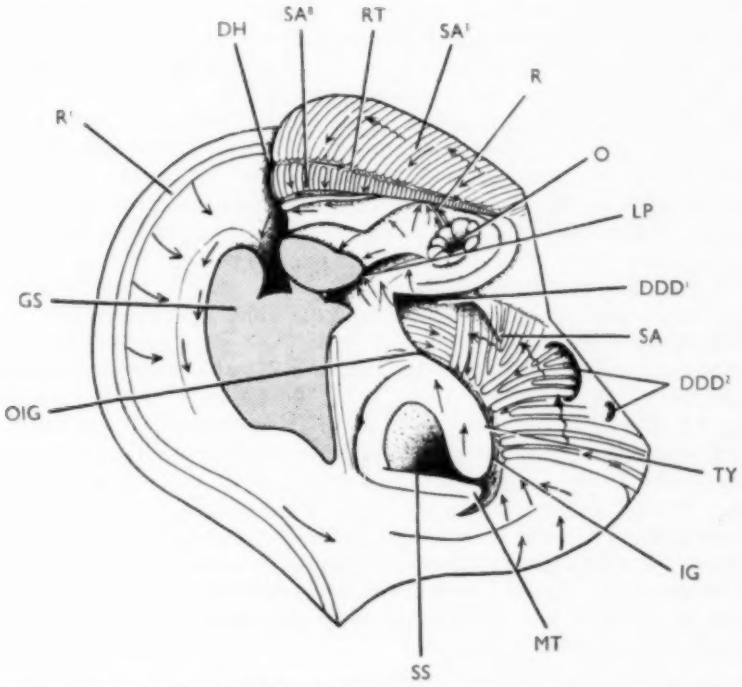

Fig. 1.—*Brechites penis*. Interior of the stomach after dissection from the right side. × 16.
(For lettering see p. 487.)

The combined style-sac (SS) and mid-gut leave the floor of the stomach and pass downwards into the visceral mass. The minor typhlosole (MT) terminates on the right side of the stomach, close to the opening of the mid-gut. The major typhlosole (TY), accompanied by the intestinal groove (IG) passes forwards over the floor of the stomach curving gradually to the left and terminates on the left anterior floor of the stomach.

The dorsal hood (DH) is large and well developed, and opens posteriorly on the left wall of the stomach. On its anterior face, dorsal to the ridge (R) which passes back from the oesophagus as described above, there are two sorting areas separated from each other by a rejection tract. On the lowermost sorting area (SA^8) cilia beat downwards in the grooves and pass particles to the ridge (R) along which they are carried towards the apex of the dorsal hood. On the uppermost sorting area (SA^3) cilia on the crests of the ridges beat transversely over the crests towards the apex of the dorsal hood, while cilia in the grooves beat downwards along the grooves and into the rejection tract (RT) which carries rejected material out of the dorsal hood and on to the right side of the stomach. The posterior wall of the dorsal hood is smooth, except for a slender ridge (R^1) which passes out of the dorsal hood and on to the posterior wall of the stomach. The dorsal hood passes forwards and steeply downwards close to the left side of the stomach.

The shallow left pouch (LP) lies antero-ventral to the orifice of the dorsal hood, and leads upwards towards the oesophagus. Powerful ciliary currents on the left anterior floor of the stomach beat into the left pouch. No ducts enter the left pouch from the digestive diverticula.

The digestive diverticula on the right side of the stomach open into the stomach by one large and one small orifice (DDD^2), both of which are invaded by the folds of a sorting area (SA) which covers the anterior floor of the stomach. Cilia on the crests of the folds beat transversely to the left over the crests, while cilia in the grooves beat posteriorly out of the orifices of the ducts from the digestive diverticula along the grooves and into the intestinal groove. The larger of these two orifices divides internally into three branches each of which receives five or six ducts from the digestive diverticula.

The digestive diverticula on the left side of the body open into the stomach by a single large orifice (DDD^1) on the left anterior wall of the stomach, anterior and ventral to that of the left pouch (LP). This chamber (DDD^1) is similarly invaded by the sorting area described above. On dissection it was found that it receives about ten ducts from the digestive diverticula, arranged in a posterior group of four ducts, a central group of three, and an anterior group of three ducts. The origin of the intestinal groove (OIG) lies on the floor of the stomach, external to the left pouch and external to the chamber (DDD^1) which receives the ducts from the digestive diverticula on the left side of the body.

The gastric shield (GS) is well developed and covers a large part of the left wall of the stomach, sending deep saddle-shaped flares into the mouths of the dorsal hood and of the left pouch.

TELLINACEA

Donacidae

Donax faba Gmelin (Fig. 2)

The long and slender oesophagus passes upwards from the mouth, and then backwards almost horizontally to its entrance on the anterior face of the stomach (O). The stout style-sac (SS) leaves the floor of the stomach and passes directly downwards into the visceral mass. The mid-gut is completely

separate from the style-sac, opening into the stomach (MG) a little in front of the orifice of the style-sac, with which it communicates by a shallow groove. There is no minor typhlosole.

The major typhlosole (TY) is well developed, and arches over the intestinal groove (IG), which accompanies it throughout its course. The major typhlosole passes forwards on to the floor of the stomach, curves gently to the left and finally passes downwards into the broad and shallow left caecum (LC) which opens on the left anterior floor of the stomach. The major typhlosole performs a loose spiral of about $1\frac{1}{2}$ turns on the posterior and median sides of the left caecum, the intestinal groove therefore originating well within the left caecum.

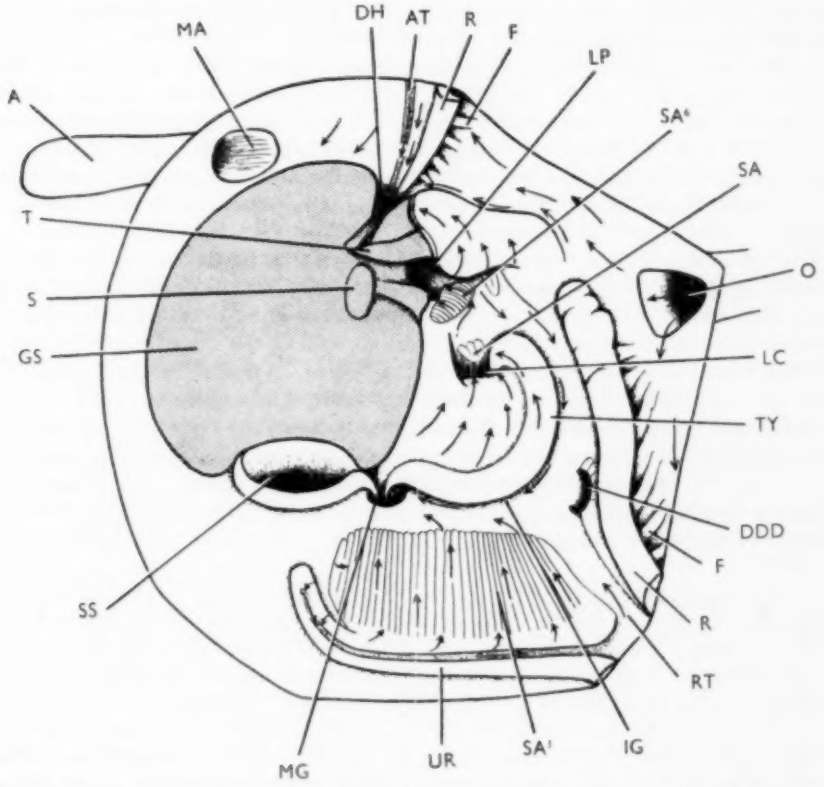

Fig. 2.—*Donax faba*. Interior of the stomach after dissection from the right side. × 15. (For lettering see p. 487.)

A sorting area (SA) of very fine ridges and grooves radiates around the spiral of the intestinal groove, into which particles are passed by the ciliary currents of the sorting area. About four ducts enter the left caecum from the digestive diverticula. Ciliary currents in these ducts are directed outwards towards the intestinal groove.

The dorsal hood (DH) forms a shallow pocket on the left side of the stomach. Its walls appear to be devoid of sorting areas, the only features being a groove (AT) in which ciliary currents pass downwards to the apex of the dorsal hood, and a conspicuous ridge (R) on its anterior wall. This ridge arises a little to the left of the median line on the anterior floor of the stomach, and passes up the right wall of the stomach, over its roof and into the dorsal hood. It projects forwards, as shown in the figure, partly hiding from view a series of large and irregular pleats (F) on the stomach wall on its anterior side. Material entering the stomach from the oesophagus is directed to the right or to the left and is carried backwards into the dorsal hood over the roof and left side of the stomach and along the upper border of the thick roll forming the roof of the left pouch. On the posterior wall of the dorsal hood cilia beat downwards and backwards, out of the dorsal hood.

The left pouch (LP) is a capacious chamber with a wide mouth that lies below and in front of the mouth of the dorsal hood. It curves backwards under the dorsal hood and receives four ducts from the digestive diverticula on the left side of the body. A long, slender sorting area (SA^6) of finely disposed transverse ridges and grooves lies on the floor of the left pouch. It extends backwards to the apex of the left pouch, and then passes forwards on the roof and left side of the left pouch.

The gastric shield (GS) covers an extensive area of the left and posterior walls of the stomach, extending down to the median border of the mouth of the style-sac. It sends a deep gutter-shaped flare into the mouth of the dorsal hood, of which the part lining the posterior wall of the dorsal hood is flimsy, while that lining the anterior wall is very firm. A well-developed tooth (T) projects backwards from the gastric shield in front of and below the mouth of the dorsal hood, and this doubtless serves to keep the tip of the crystalline style in position. Immediately below this tooth the gastric shield is developed into an oval opaque white swelling (S). The gastric shield sends a long and strong flare into the mouth of the left pouch. This flare is relatively slender, and it curves backwards along the posterior wall of the left pouch to its apex.

The appendix (A) is long, cylindrical and thin walled. It opens into the stomach by a wide mouth (MA) situated just behind that of the dorsal hood. The appendix passes backwards and downwards immediately above the roof and posterior wall of the stomach. The interior of the appendix is finely grooved, due doubtless to contraction of its muscular walls.

The digestive diverticula on the right side of the stomach open into the stomach by two or three large ducts which join to form a single large orifice (DDD) in the stomach wall low down on the right anterior wall. This orifice is protected from material passing backwards into the stomach from the oesophagus by the well-developed ridge (R) which has been described above. There are no isolated ducts from the digestive diverticula on the right side of the stomach. It is notable that the major typhlosole and the accompanying intestinal groove do not invade the orifice (DDD) by which the digestive diverticula of the right side open into the stomach. This condition is not found in other families in the Tellinacea, which are described below.

There is a sorting area (SA^3) on the right side of the stomach, consisting of a series of fine ridges and grooves which run down at right angles towards the intestinal groove (IG). Ciliary currents on this sorting area pass down the grooves to the intestinal groove. No trace could be found of any current passing transversely over the crests of the folds towards the dorsal hood, and it is concluded that this area serves solely for trapping and rejecting waste material into the mid-gut. The upper border of this sorting area is marked by a " U "-shaped ridge (UR), the two arms of which project forwards. In the groove between the arms there is a forwardly directed ciliary current which passes material up to the dorsal hood. A rejection tract (RT) passes downwards from the dorsal hood towards the intestinal groove. This rejection tract lies on the anterior border of the above mentioned sorting area (SA^3).

Yonge (1949) figured and described the stomach of *Donax vittatus*, in which he showed that the style-sac and mid-gut are separate.

STOMACH TYPE V

The diagnostic feature of this type of stomach is the extension of the major typhlosole and the intestinal groove into two caeca, one on the right side of the oesophageal orifice and one on the left. It has been suggested that this is typical of the majority of the Eulamellibranchia (Owen, 1953 ; Morton, 1958) but this is not correct. Of all the families of Eulamellibranchia which have been studied in this respect only about one half possess a stomach of Type V, the stomach in the remainder being of Type IV (Purchon, 1958).

Definition of Type

1. The oesophagus enters on the anterior side of the stomach.

2. The style-sac and mid-gut are usually conjoined (the Dreissenidae, Mactridae, Mesodesmatidae, Solenidae, Myidae and Pholadidae are exceptional) and leave the ventral or posterior wall of the stomach.

3. There is a crystalline style which projects across the stomach, presses into the mouth of the dorsal hood, and probably rotates in a clockwise direction when viewed from the anterior end.

4. The dorsal hood is relatively large and there is a well-developed sorting area on its anterior wall. The mouth of the dorsal hood is invested by lobes of the gastric shield.

5. The minor typhlosole terminates on the right wall of the stomach close to the orifice of the mid-gut, except for the families in which the mid-gut and style-sac are separate, in which the minor typhlosole is apparently absent.

6. The major typhlosole passes forwards from the mid-gut into the stomach, accompanied on its right side by the intestinal groove. Both structures pass into and circumnavigate a right caecum, emerge from the caecum on its anterior side and cross the anterior floor of the stomach from right to left. Both structures then enter a left caecum on its anterior side and circumnavigate the caecum. Within the left caecum the major typhlosole and intestinal groove may make a simple U-shaped turn and terminate just inside or just outside the mouth of the left caecum, or the typhlosole and intestinal

groove may form a loose spiral (e.g. Tellinidae) or a tight spiral (e.g. Tridacnidae) within the left caecum. *Chama lazarus* (Chamidae) is exceptional in that the major typhlosole forms three tongues within the left caecum and two tongues on the right side of the stomach, one of which enters the right caecum and the other enters an accessory right caecum.

7. There is a left pouch on the left anterior wall of the stomach, and its posterior border is invested by a lobe of the gastric shield. The left pouch typically receives one or more ducts from the digestive diverticula.

8. The principal sorting area of the dorsal hood (SA^3) is almost invariably present and the sorting areas in the left pouch (SA^6) and on the anterior roof of the stomach (SA^8) are commonly present. There is considerable variation in the extent of these sorting areas in the different families and genera, doubtless related to the habitat, growth form, and source of food. Sorting areas are occasionally found on the posterior wall of the dorsal hood (SA^5) and immediately below the oesophageal orifice (SA^7), and on rare occasions in other parts of the stomach.

9. In addition to the ducts which enter the left pouch, left caecum and right caecum, a number of ducts from the digestive diverticula open independently on the right side of the stomach in about a half of the families studied. The number of such independent ducts may vary considerably, even within a genus.

10. A rejection tract carries material out of the dorsal hood, down the right side of the stomach and discharges it into the intestinal groove.

Description of Material

SPHAERIACEA

Corbiculidae

Geloina ceylanica Lamarck (Fig. 3)

The stomach is large and globular, with a forward prolongation into which the oesophagus (O) opens. The stomach is surrounded anteriorly by a large mass of orange coloured digestive diverticula and posteriorly by a grey coloured gonad. The orifice by which the oesophagus opens into the stomach is marked by a well-defined transverse ridge (RM). There is a small sorting area on the anterior floor of the stomach (SA), immediately below the oesophageal orifice, and extending a short distance backwards on the right side of the stomach below the acceptance tract (G).

The style-sac (SS) and mid-gut (MG) are conjoined and pass vertically downwards from the postero-ventral wall of the stomach. The minor typhlosole terminates on the posterior rim of the opening of the mid-gut. The major typhlosole (TY) passes forwards over the floor of the stomach, arching over a deep intestinal groove (IG). It sends a large frilled lobe into the right caecum (RC) which passes far downwards and backwards into the digestive diverticula, which open into it by at least fourteen orifices. The major typhlosole sends small flares into the mouths of all of these ducts. The major typhlosole emerges from the right caecum and passes to the left across the

anterior floor of the stomach, being there developed into a large forwardly directed lobe (TY^1). It then passes into the mouth of the left caecum (LC), which is almost as deep as the right caecum, and which receives about ten ducts from the digestive diverticula. The major typhlosole penetrates to its apex, sending flares into the mouths of all of the ducts from the digestive diverticula. The major typhlosole and the accompanying intestinal groove pass up the posterior wall of the left caecum, emerging on its posterior border, and the origin of the intestinal groove (OIG) is on the left floor of the stomach, just posterior to the mouth of the left caecum. A portion of the sorting area (SA) leads down the left side of the stomach towards the origin of the intestinal groove (OIG), into which it directs particles.

The dorsal hood (DH) is very large and well developed ; its mouth is invested by lobes of the gastric shield (GS), and it projects forwards on the left side of the stomach. The left and posterior side of the dorsal hood is

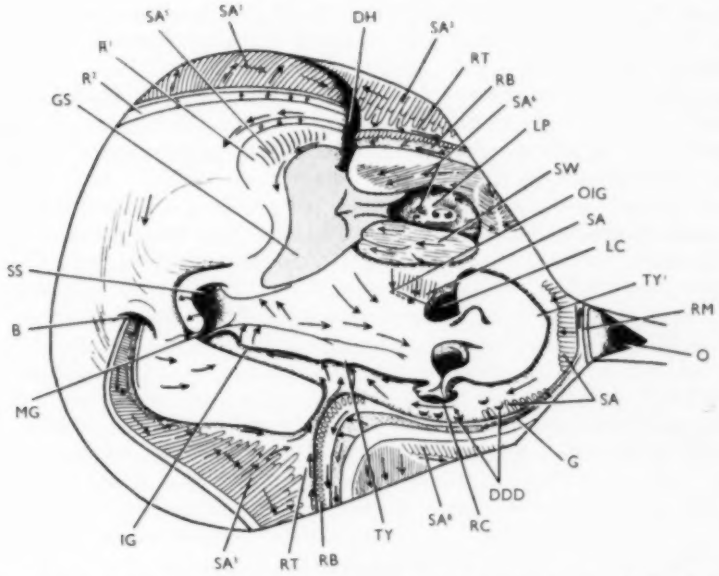

Fig. 3.—*Geloina ceylanica*. Interior of the stomach after opening by a mid-dorsal incision. (For lettering see p. 487.)

relatively smooth, with a broad ridge (R^1) adjacent to the border of the gastric shield. On this ridge there are some regular transverse striations which might be deemed to constitute a sorting area (SA^5). The upper margin of the smooth area is also bordered by a ridge (R^2) which is comparatively slender. Above this slender ridge, and on the roof of the dorsal hood there is a well-developed sorting area (SA^3) of fine transverse ridges and grooves. Cilia in the grooves beat along the grooves away from the ridge (R^2) towards the anterior side of the dorsal hood, while cilia on the

crests of the folds beat transversely over the crests and inwards to the apex of the dorsal hood. This sorting area extends over the roof of the stomach and down its right side, terminating in a small blind pocket (B) on the right posterior wall, close to the orifice of the mid-gut. Material rejected from this sorting area is passed into a rejection tract (RT) which arises within the dorsal hood, and which discharges into the intestinal groove (IG).

The left pouch (LP) is a large, well-defined oval cavity the posterior border of which is invested by a very firm saddle-shaped lobe of the gastric shield (GS). On the median side of the left pouch there is a large fleshy swelling (SW) on the left side of the stomach. Cilia on this swollen area beat backwards, towards the gastric shield. The digestive diverticula on the left side of the stomach open into the left pouch by five orifices, and an irregular sorting area (SA^6) extends over the wall of the left pouch, between these orifices. This sorting area extends over the roof of the left pouch and on to the left wall of the stomach. Here cilia beat backwards along the grooves, towards the upper border of the gastric shield and past this into the dorsal hood. A further sorting area (SA^8) lies on the anterior roof of the stomach, anterior to the roof of the left pouch.

In addition to the ducts from the digestive diverticula which open into the stomach via the left pouch, the left caecum and the right caecum, as described above, five ducts (DDD) open separately on the right side of the stomach, just above the mouth of the right caecum.

On the roof of the stomach anteriorly there is a groove (G) which leads backwards, between two slender ridges, towards and into the dorsal hood. Cilia in this groove beat backwards and carry particles from the oesophagus into the dorsal hood. This may therefore be regarded as an acceptance tract. It is separated from the rejection tract (RT), described above, by a fleshy ridge which is ornamented by a series of oval beads (RB).

In general the walls of the stomach are thin and flabby, but considerable muscular action was noted at two points, where fairly rapid and extensive contractions were observed. These points were the orifices of the left pouch (LP) and of the blind pocket (B) on the right posterior wall of the stomach.

CORBICULIDAE

Corbicula japonica Prime

Dissections were made of specimens which had been fixed in Bouin's fluid and preserved in 70 per cent alcohol. The interior of the stomach was filled with a firm matrix which was probably derived from the substance of the crystalline style. The fine structure of the interior of the stomach was admirably preserved and, although it was not possible to make a well-proportioned drawing due to brittleness of the thin stomach wall, it was possible to determine the major structural features.

The oesophagus enters the stomach anteriorly, and the combined style-sac and mid-gut leave the stomach posteriorly. The major typhlosole passes

directly forwards over the floor of the stomach, and sends an extensive, frilled tongue into the right caecum, which passes downwards and backwards below the right side of the stomach. The major typhlosole crosses the stomach transversely and enters the left caecum, penetrating it deeply and terminating just within the mouth of the left caecum, on its posterior side.

The dorsal hood is well developed, and passes transversely over to the left of the stomach. Its anterior face bears an extensive sorting area (SA^3) of transverse ridges and grooves, bordered on each side by a longitudinal ridge. This sorting area passes over the roof and on to the right side of the stomach, where it passes backwards to the vicinity of the mouth of the mid-gut. Below this sorting area in the dorsal hood, and adjacent to the flare of the gastric shield, there is a thick longitudinal ridge (R) which is sub-divided into a series of beads by transverse grooves. This ridge terminates on the right side of the stomach, close to the mouth of the right caecum. The posterior face of the dorsal hood is mostly smooth, but a series of longitudinal grooves leads downwards from the dorsal hood over the posterior wall of the stomach, towards the orifice of the style-sac.

The left pouch lies anterior and ventral to the dorsal hood. There is a well-defined sorting area (SA^6) of closely arranged transverse folds on the roof of the left pouch, and also an irregular sorting area on its floor. There is a swelling on the floor, in the mouth of the left pouch. Three ducts enter the left pouch from the digestive diverticula, one on its outer wall, and two near its apex.

There do not seem to be any isolated ducts from the digestive diverticula on the right side of the stomach. The gastric shield is well developed, and sends strong flares into the mouths of the dorsal hood and the left pouch.

Villorita cyprinoides (Gray)

The interior of the stomach of *V. cyprinoides* var. *cochinensis* (Hanley) has been figured and described by Dinamani (1957). It is clear from this account that the stomach of *Villorita* is of Stomach Type V. The main features of the stomach are as follows : The style-sac and mid-gut are conjoined. One or two isolated ducts from the digestive diverticula open into the stomach on its right side, immediately above the mouth of the right caecum. It is possible that a single duct from the digestive diverticula opens into the left pouch. Only two large sorting areas are recorded. The larger of these ($=SA^3$) lies on the right side of the stomach, extends into the dorsal hood, and is typical in all respects save that Dinamani did not find any trace of ciliary currents passing transversely over the crests of the folds towards the apex of the dorsal hood. The other sorting area ($=SA^6$) lies on a fleshy swelling that forms the floor of the left pouch and overhangs the mouth of the left caecum. The origin of the intestinal groove appears to be on the floor of the stomach, just outside the mouth of the left caecum, adjacent to a small sorting area which directs particles into the intestinal groove. In both the left caecum and the right caecum the ducts from the digestive diverticula open in groups of three or four into each of five recesses in the caecal wall.

CHAMACEA

Chamidae

Chama lazarus L. (Fig. 4)

The slender oesophagus opens by a small circular orifice (O) into a hemispheric anterior chamber, or vestibule (V) of the stomach. The conjoined style-sac (SS) and mid-gut leaves the postero-ventral wall of the stomach, and the minor typhlosole (MT) terminates on the right wall of the stomach, close to the mouth of the mid-gut. The major typhlosole (TY) is small and flimsy, and passes forwards from the mid-gut on to the floor of the stomach. It sends a semi-circular flare into a shallow pocket on the right side of the stomach, into which open three ducts from the digestive diverticula. This pocket, for lack of any better definition, may be termed the " accessory right caecum " (ARC). Emerging from the accessory right caecum, the major typhlosole, accompanied by the intestinal groove (IG) passes forwards to the mouth of the right caecum (RC) into which it sends a long, slender tongue.

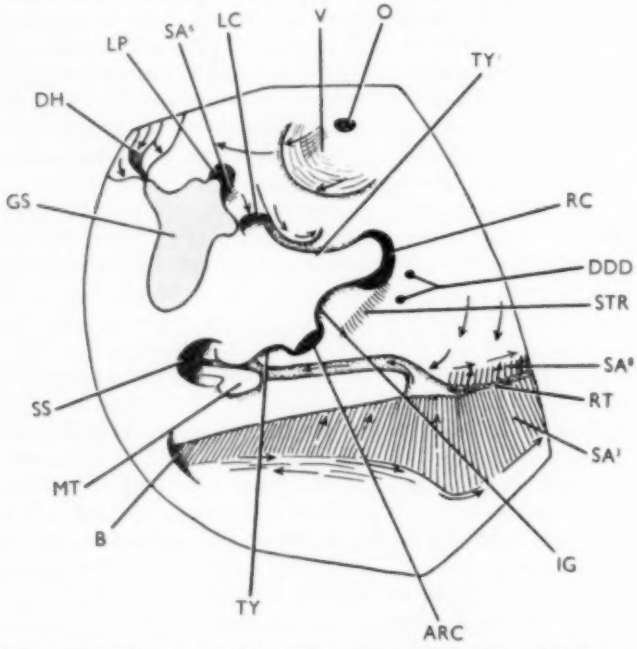

Fig. 4.—*Chama lazarus*. Interior of the stomach after opening by an oblique incision in the right side. (For lettering see p. 487.)

The right caecum curls far forwards around the anterior side of the stomach, and the tongue of the major typhlosole penetrates to its apex. Seven or eight ducts enter the right caecum from the digestive diverticula.

The major typhlosole and intestinal groove emerge from the right caecum on its anterior side, cross the floor of the stomach transversely (TY^1) and enter

the left caecum (LC), the mouth of which is situated on the left anterior floor of the stomach. Within the left caecum the major typhlosole is remarkable in that it divides to form three slender tongues, each at least twice as long as it is broad, of which one points forwards and the others are directed backwards. The main part of the left caecum passes downwards under the stomach. The major typhlosole and the intestinal groove terminate deep within the left caecum. Numerous ducts enter the left caecum from the digestive diverticula.

The left pouch (LP) lies on the left anterior side of the stomach, its mouth lying a little above and behind that of the left caecum. The left pouch is small, rounded, and well defined ; it receives five ducts from the digestive diverticula on the left side of the body. A sorting area (SA^6) of finely disposed ridges and grooves lies on its floor and projects slightly on to the left wall of the stomach. Ciliary currents on this sorting area pass away from the orifices of the ducts of the digestive diverticula, along the grooves of the sorting area towards the gastric shield.

In addition to the ducts which open into the left pouch, the left caecum, the right caecum and the " accessory right caecum ", the digestive diverticula also communicate with the stomach by two isolated ducts (DDD) on the right side of the stomach.

The dorsal hood (DH) is relatively small, and is situated on the left side of the roof of the stomach. It is penetrated by two sorting areas, on which the ciliary currents are powerful. These consist of a large sorting area (SA^3) on the roof of the dorsal hood, which passes over the roof of the stomach and far backwards on its right side, terminating in a small blind pocket (B). Ciliary currents on the crests of the folds pass transversely over the folds towards the apex of the dorsal hood. Cilia in the grooves beat along the grooves and into a rejection tract (RT) which passes down from the dorsal hood and discharges material into the intestinal groove. The second sorting area (SA^8) lies anterior to the rejection tract, and passes up the right wall of the stomach, over its roof and on to the anterior wall of the dorsal hood. On the anterior side of this sorting area there is an acceptance tract which conveys material towards the apex of the dorsal hood. Cilia on the left wall of the vestibule (V) beat strongly backwards, past the upper border of the left pouch and into the dorsal hood on its anterior side.

The gastric shield (GS) is relatively small, but has a well-developed tooth which holds the tip of the crystalline style in position. The gastric shield sends a spout-like projection into the mouth of the dorsal hood, and it also invests the posterior border of the left pouch with a flare.

There is a very faint system of parallel striations on the right wall of the right caecum, and this system emerges from the right caecum on to the wall of the stomach (STR).

This stomach has been assigned to Stomach type V, but it must be emphasized that it is atypical in two respects. There is an accessory right caecum which may have arisen by this structure breaking away from the right border of the right caecum ; this interpretation is rendered the more probable by reference to the second peculiarity, which is the branching of the tongue of the major typhlosole in the left caecum. The same branching may have

occurred in the right caecum, followed by the isolation of the first branch of the tongue into a separate " accessory right caecum ".

DREISSENACEA

Dreissenidae

Dreissena polymorpha Pallas (Fig. 5)

The large and thin-walled stomach lies close to the surface of the visceral mass, and the short and wide oesophagus (O) enters antero-ventrally. The style-sac (SS) and the mid-gut (MG) are separate. The style-sac enters the stomach by a circular opening on its posterior wall, a little to the left of the median line, and curves backwards to the posterior end of the visceral mass. The mid-gut opens into the stomach a little to the right and slightly in front of the orifice of the style-sac. The mouths of the style-sac and of the mid-gut communicate by a short groove (GR) lying between two fleshy ridges.

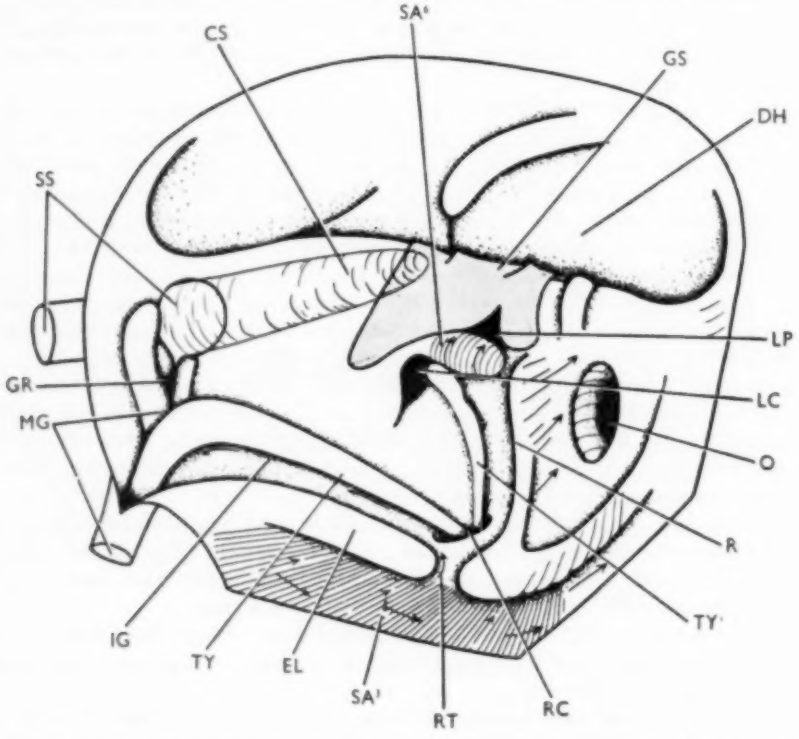

Fig. 5.—*Dreissena polymorpha*. Interior of the stomach after opening by a horizontal incision in the right side. (For lettering see p. 487.)

The relatively large and fleshy major typhlosole (TY) passes forwards over the floor of the stomach from the mouth of the mid-gut towards the right

caecum (RC), which it penetrates deeply. Emerging from the anterior side of the right caecum, the major typhlosole passes transversely across the anterior floor of the stomach (TY^1) and enters the left caecum (LC) on its anterior side. It penetrates the left caecum deeply, and terminates within it. The major typhlosole is accompanied throughout its course by the intestinal groove (IG). Numerous ducts from the pale digestive diverticula open into the stomach via the left caecum and the right caecum.

The dorsal hood (DH), which opens into the stomach by a very wide mouth, forms a short forward projection on the left anterior side of the stomach. Immediately below the mouth of the dorsal hood there is a left pouch (LP), which is a deep pocket into which open four ducts from the digestive diverticula on the left side of the body. A sorting area (SA^6) extends over the floor of the left pouch, and on to a fleshy swelling which lies outside the left pouch, between it and the left caecum. Cilia on this fleshy swelling beat along the grooves of the sorting area and into the left pouch.

The gastric shield (GS) lies on the left side of the stomach and sends lobes into the mouths of the dorsal hood and of the left pouch.

A sorting area (SA^3) of ridges and grooves covers the right wall of the stomach and extends upwards into the dorsal hood. Postero-ventrally it is separated from the intestinal groove by a broad forward projecting elevation (EL) from the region of the opening of the mid-gut. Anteriorly it is bordered on its median side by a thick lobed ridge which bends sharply to the left and crosses the anterior floor of the stomach transversely from right to left (R) forming a backwardly directed flap here, which protects the transverse part of the intestinal groove from material entering the stomach from the oesophagus. Cilia on the crests of the ridges of this sorting area (SA^3) beat transversely over the crests, forwards and into the dorsal hood. Cilia in the grooves of this sorting area beat along the grooves and discharge material via a rejection tract (RT) into the intestinal groove (IG).

LUCINACEA

Ungulinidae

Diplodonta spp.

Allen (1958) gave an illustrated account of the stomachs of *Diplodonta rotundata*, *D. semiaspera* and *D. punctata*, his account being easily equated with the present survey. Variation in the number of ducts which open independently on the right side of the stomach is striking, there being seven such ducts in *D. rotundata*, four in *D. punctata* and only one in *D. aspera*. Regarding the sorting areas, the posterior sorting area in the dorsal hood (PSA in Allen's Fig. 43) is here called the principal sorting area of the dorsal hood (SA^3). The ridged area " on the left side of the gastric shield " (GP in Allen's Fig. 43) apparently lies on the *anterior* side of the gastric shield and stretches from the mouth of the left caecum upwards to that of the left pouch. This is therefore the sorting area of the left pouch (SA^6). Finally the ridged area posterior to the orifice of the oesophagus, judging by the direction of the ciliary currents, is apparently a sorting area (SA^7).

ISOCARDIACEA

Isocardiidae

Glossus humanus (L.)

The structure and function of the interior of the stomach of *G. humanus* has been illustrated and described in detail by Owen (1953), and no further description is required.

CYPRINACEA

Cyprinidae

Cyprina islandica (L.) (Fig. 6)

The long and slender oesophagus enters the stomach antero-dorsally (O), its orifice into the stomach being marked by a transverse ridge (RM) on which cilia beat transversely away from the median ventral line and on to the anterior roof of the stomach, where a ciliary tract (G) collects particulate material and conveys it backwards into the dorsal hood. Since cilia on the anterior floor of the stomach beat forwards towards the transverse ridge all material entering the stomach from the oesophagus must first be passed to the dorsal hood.

The combined style-sac (SS) and mid-gut pass downwards from the posterior wall of the stomach. The minor typhlosole (MT) bends sharply to the right on entering the stomach, and terminates close to the mouth of the mid-gut. A broad groove which lies immediately in front of the end of the minor typhlosole constitutes a ciliary rejection groove (RG) discharging into the intestinal groove (IG).

The major typhlosole (TY), accompanied by the intestinal groove (IG), passes directly forwards over the floor of the stomach and sends a very broad and long tongue into the right caecum (RC), into which open about eight ducts from the digestive diverticula. The tongue of the typhlosole sends a small flare into the mouth of each of these ducts. There are powerful ciliary currents on the upper surface of this tongue of the major typhlosole in the mouth of the right caecum. Laterally the cilia beat strongly into the right caecum, while on the median side of the tongue the cilia beat outwards, from the right caecum and across the stomach floor to the left. It seems probable that in *Cyprina*, as also in *Glossus* (Owen, 1953), particles are carried directly to the orifices of the ducts of the digestive diverticula by ciliary currents, whereas in many other cases, e.g. the Pholadidae (Purchon, 1955, 1956) the ciliary currents in the vicinity of the ducts are directed away from the ducts and towards the stomach. The major typhlosole crosses the anterior floor of the stomach from right to left (TY^1) and passes into the left caecum (LC), which is of about the same size as the right caecum. It is penetrated by a deep broad tongue of the major typhlosole, which emerges from the left caecum on its posterior side, so that the origin of the intestinal groove (OIG) is on the left floor of the stomach, just outside the left caecum.

The mouth of the dorsal hood (DH) is a horizontal slit on the left side of the stomach, near the mid-dorsal line. The dorsal hood is broad and blunt,

and coils downwards and backwards close to the left side of the stomach, and then it turns forwards towards its apex which lies below the level of its orifice into the stomach. Particles enter the dorsal hood on its anterior side, and are carried out of the dorsal hood by a strong ciliary current on its roof, and by a weak ciliary current on the posterior wall of the dorsal hood.

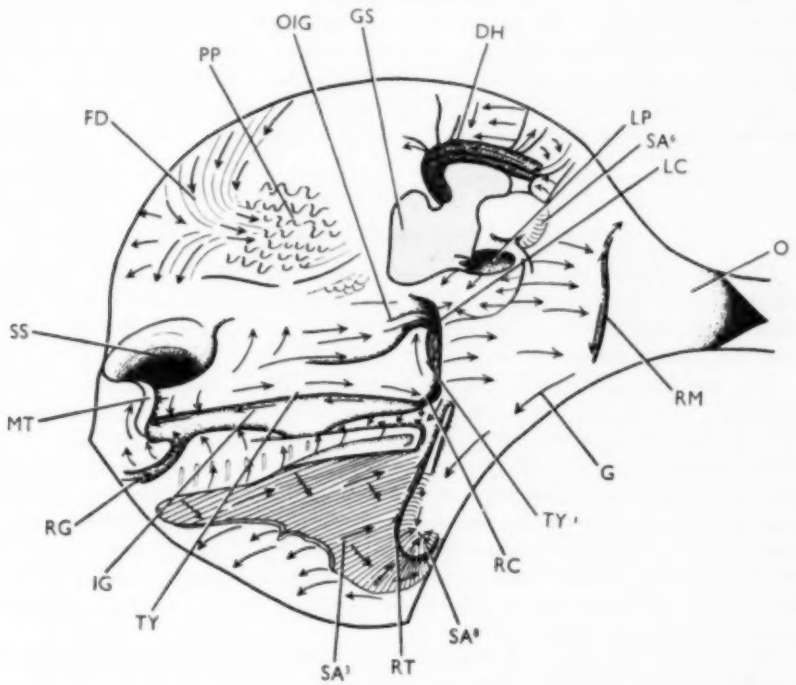

Fig. 6.—*Cyprina islandica*. Interior of the stomach after opening by a mid-dorsal incision (For lettering see p. 487.)

There is a well-developed left pouch (LP), which receives about nine ducts from the digestive diverticula. The mouth of the left pouch lies on the left wall of the stomach, below that of the dorsal hood. The gastric shield (GS) is thin and flimsy ; it invests the posterior floor of the mouth of the dorsal hood, and it sends a long, but flimsy extension into the mouth of the left pouch. A sorting area (SA^6) emerges from the roof of the pouch.

There is an extensive sorting area (SA^3) on the right wall of the stomach, and reaching up to the anterior wall of the dorsal hood. Cilia in the grooves of this sorting area beat along the grooves and into a rejection tract (RT), which runs along the anterior border of the sorting area and which discharges into the intestinal groove (IG). Cilia on the crests of the folds beat transversely over the crests, upwards and into the dorsal hood. Anterior to the rejection

tract (RT) there is a second, but smaller sorting area (SA^8) which passes upwards and forwards in a loose spiral towards the anterior side of the mouth of the dorsal hood. On the anterior side of this sorting area cilia beat upwards and into the dorsal hood.

On the left posterior wall of the stomach there is a series of irregular folds (FD) which converge on an area of irregular rows of papillae (PP). Cilia in the grooves of this sorting area beat towards the papillae. Material that collects in this region will probably be pressed against the crystalline style. Ciliary currents on the posterior floor of the stomach are particularly powerful, and direct particles forwards and to the right or to the left and into the right or left caecum respectively. The most notable feature of the stomach of *Cyprina* is the great extent and vigour of ciliary activity.

Libitinidae

Trapezium sublaevigatum Lamarck (Fig. 7)

The oesophagus enters the antero-ventral face of the stomach. The oesophageal orifice is separated from the intestinal groove by a transverse ridge which stretches to the right from the anterior border of the left pouch. (This ridge cannot be seen in Fig. 7.)

The combined style-sac (SS) and mid-gut leave the stomach postero-ventrally. The minor typhlosole (MT) ends on the right wall of the stomach, close to the orifice of the mid-gut. The major intestinal typhlosole (TY), accompanied by the intestinal groove (IG), passes forwards over the floor of the stomach and enters the right caecum (RC), which it penetrates deeply and from which it emerges on the anterior side. The major typhlosole then passes transversely across the anterior floor of the stomach (TY^I) and enters the left caecum (LC), which it also penetrates deeply, emerging on to the floor of the stomach on the posterior side of the mouth of the left caecum, where the intestinal groove originates (OIG).

The dorsal hood (DH) lies anteriorly, with its mouth stretching over the roof of the stomach, in much the same way as in *Petricola pholadiformis* (Purchon, 1955 a) so that in Fig. 7 the floor of the dorsal hood—which is morphologically its anterior side—obscures from view the opening of the oesophagus into the stomach.

There are two sorting areas of ridges and grooves on the floor—or anterior wall—of the dorsal hood. The larger of these (SA^3) extends from the apex of the dorsal hood on to the right side of the stomach. Here cilia on the crests of the folds beat very weakly transversely over the crests and towards the apex of the dorsal hood, while cilia in the grooves beat along the grooves and into a rejection tract (RT) which passes along the posterior border of the sorting area and discharges down the right side of the stomach into the intestinal groove (IG). The smaller sorting area (SA^8) lies on the posterior side of this rejection tract, and extends from the apex of the dorsal hood across the mouth of the dorsal hood on to the right side of the stomach, where it terminates above and behind the mouth of the right caecum (RC). On this sorting area cilia beat backwards in the grooves and into an acceptance tract

which runs along the posterior border of the sorting area towards the apex of the dorsal hood.

There is a moderately large sorting area (SA^5) on the roof—or posterior wall—of the dorsal hood. Here cilia beat upwards in the grooves into a ciliated tract which lies along the upper border of the sorting area, and which conveys material out of the dorsal hood. This material probably passes down the posterior part of the right wall and into the intestinal groove.

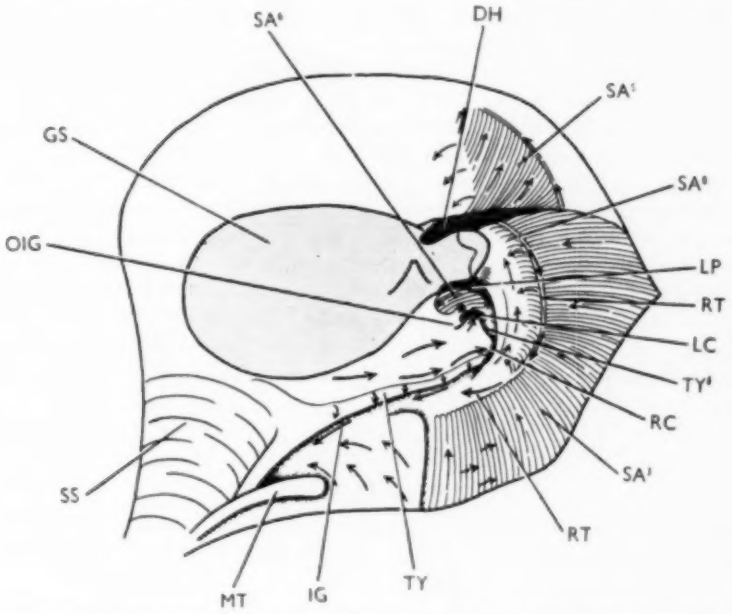

Fig. 7.—*Trapezium sublaevigatum*. Interior of the stomach after opening by an oblique incision in the right wall from the mouth of the dorsal hood to the mid-gut. (For lettering see p. 487.)

The left pouch (LP) lies on the left anterior wall of the stomach, immediately above the mouth of the left caecum. There is a sorting area (SA^6) on the floor of the left pouch, which extends over the floor of the left pouch and a short distance up its left wall towards the mouth of the dorsal hood. This sorting area spreads over a conspicuous bulge in the mouth of the left pouch. Three ducts from the digestive diverticula enter the stomach on the median side of this bulge, and others open into the deeper parts of the left pouch.

The relatively large gastric shield (GS) spreads over the left wall of the stomach, where it is very firmly held. It sends flares into the mouths of the dorsal hood and of the left pouch.

In addition to the ducts from the digestive diverticula which enter the stomach via the left pouch as mentioned above, a number of ducts enter the left caecum, and about six enter the right caecum. Three ducts open independently on the right wall of the stomach, dorsal to the orifice of the right caecum.

CARDIACEA

Cardiidae

Cardium edule L.

Graham (1949) gave a general description and illustration of the interior of the stomach of *C. edule*, and referred to the previous work on the stomach of this species by Johnstone (1899). It is abundantly clear from the above description that the stomach of *C. edule* is of Type V. Graham recorded that the digestive diverticula on the right side of the stomach open into the stomach by one duct which opens separately (not shown in his Fig. 12) and by nine ducts which enter the right caecum. The number of ducts which enter the left caecum was not stated, but it was suggested that at least nine ducts enter here. It was stated that ducts from the digestive diverticula discharge into the left pouch, but the number was not specified. The style-sac and mid-gut are conjoined, and the dorsal hood is evidently rather small.

Graham described two sorting areas in *C. edule*. One of these, on the posterior half of the right wall of the stomach (=SA^3) consists of rather broad and well-spaced ridges, and leads up the right side of the stomach towards the mouth of the dorsal hood. Material from this sorting area is discharged into the intestinal groove. The other sorting area (=SA^7), which lies between the orifice of the oesophagus and the transverse part of the major typhlosole, consists of exceedingly fine ridges and grooves, as was confirmed by the present writer.

Tridacnidae

Tridacna crocea Lam.

Reference should be made to the recent illustrated account of the structure and function of the stomach of *T. crocea* (Purchon, 1955 b) to which no further information can as yet be added.

VENERACEA

Veneridae

Gafrarium minimum (Montagu) (Fig. 8)

The oesophagus (O) enters the globular stomach on its antero-dorsal face, the oesophageal orifice being marked by a transverse rim (RM). The combined style-sac (SS) and mid-gut passes directly downwards into the visceral mass from the floor of the stomach, while a well-developed dorsal hood (DH) projects upwards from the roof of the stomach and curves over towards the left side. The minor intestinal typhlosole (MT) terminates on the right side of the stomach, close to the orifice of the mid-gut. The major typhlosole (TY), accompanied by the intestinal groove (IG), passes forwards over the floor of the stomach and sends a tongue vertically downwards into the lower part of the right caecum (RC), which is situated close to the median line. The major typhlosole (TY^1) emerges from the right caecum and passes across the floor of the stomach to the left, forming a flap which projects forwards towards the oesophageal orifice. This transverse part of the major typhlosole is relatively

narrow, since the left caecum and right caecum are placed unusually close ot the median line. The major typhlosole passes into the left caecum (LC), which it penetrates in the usual manner, and returns towards the lumen of the stomach, the origin of the intestinal groove (OIG) lying on the left anterior floor of the stomach, close to the mouth of the left caecum.

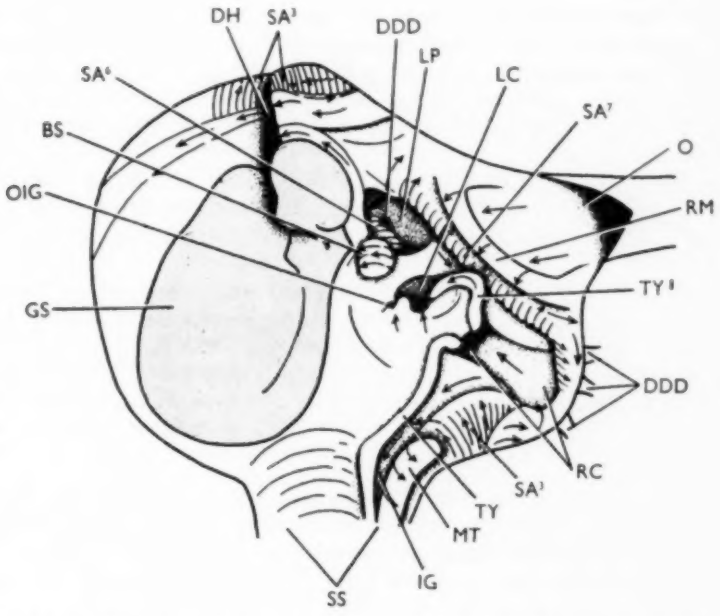

Fig. 8.—*Gafrarium minimum*. Interior of the stomach after opening by a mid-dorsal incision passing from the oesophagus to the mid-gut. (For lettering see p. 487.)

The left caecum is relatively short, and receives four ducts from the digestive diverticula, one of these opening on its posterior wall close to the origin of the intestinal groove, two opening on its ventral, and one on its anterior wall. Ciliary currents in the left caecum are directed away from the orifices of these ducts and towards the intestinal groove.

The right caecum (RC) may be considered as consisting of two parts. The lowermost of these passes directly downwards, close to the median line, and receives a tongue of the major typhlosole as mentioned above. Four ducts enter this part of the right caecum. The other part of the right caecum passes upwards and forwards and is not associated with the major typhlosole or the intestinal groove. This part of the right caecum receives three ducts from the digestive diverticula (DDD). These two parts of the right caecum are placed in communication by a broad channel on which cilia beat downwards, towards the major typhlosole.

The upper group of ducts from the digestive diverticula could alternatively be regarded as opening into the stomach independently of the right caecum.

The left pouch (LP) opens into the stomach on its left anterior wall, above the mouth of the left caecum. A sorting area (SA^6) on the floor of the left pouch passes on to the left side of the stomach, where it expands slightly to form a beaded swelling (BS). Three ducts (DDD) enter the left pouch from the digestive diverticula on the left side of the body. Cilia on the sorting area beat backwards along the grooves, away from the mouths of the ducts.

The dorsal hood (DH) is well developed, and curves to the left side from the roof of the stomach. A sorting area (SA^3) on its roof and anterior face passes over to the right wall of the stomach, posterior to the orifice of the right caecum, and cilia in the grooves of this sorting area pass material into the intestinal groove.

The gastric shield (GS) covers an extensive area on the left wall of the stomach, sends a deep saddle-shaped flare into the mouth of the dorsal hood, covering its lower border, and a deep flare invests the posterior border of the left pouch.

There is a sorting area (SA^7) on the anterior wall of the stomach, between the orifice of the oesophagus and the transverse part of the intestinal groove. Cilia here beat upwards, towards the oesophagus. This sorting area extends to the upper border of the right caecum, where cilia beat along the grooves from right to left, and probably convey material towards the dorsal hood.

Dosinia lupinus (L.)

The interior of the stomach of *D. lupinus* is fundamentally the same as that of *Gafrarium minimum*, and an additional illustration is not necessary. The chief features of interest of the stomach of *Dosinia* are as follows. The digestive diverticula open by about eight ducts which enter the left pouch, at least eight which enter the left caecum and by four large and a few small ducts which enter the right caecum. There are no isolated ducts on the right side of the stomach. The principal sorting area of the dorsal hood (SA^3) which is well developed, consists of alternating long and short ridges as in *Geloina ceylanica* (Fig. 3) and extends further over the right wall of the stomach than in *Gafrarium*. The other sorting area on the anterior wall of the dorsal hood (SA^8), which was not identified in *Gafrarium*, is well developed in *Dosinia*, where it passes over the roof of the stomach, down its right side, and joins the sorting area (SA^7) immediately below the orifice of the oesophagus.

Venus fasciata (da Costa)

Paphia pullastra (Montagu)

Graham (1949) described the interior of the stomachs of these two species, and gave an illustration for that of *P. pullastra*. Some changes in nomenclature and in interpretation are required to bring the detailed descriptions of Graham into harmony with the present survey. Thus the "dorsal pouch" of Graham is here referred to as the "dorsal hood", as recommended by Owen (1953) and Purchon (1955). Similarly the "left half of the caecum"

and the " right half of the caecum " are here termed the " left caecum " and the " right caecum " respectively. Graham considered that the digestive diverticula were divided into left and right lobes, and that those of the left lobe discharged into the stomach via the left pouch, while those of the right lobe discharged partly into the left caecum and partly into the right caecum. The present writer sees no grounds for holding that the digestive diverticula can be considered as consisting of left and right moieties.

Glaucomyidae

Glauconome rugosa Reeve (Fig. 9)

The stomach is elongated and lies very close to the hinge line, with a large mass of dark green digestive diverticula pressed against it anteriorly and antero-laterally. The broad and smooth oesophagus enters the stomach anteriorly (O), its orifice into the stomach being marked by a transverse ridge (RM). There is a second transverse ridge, a little behind the first, though this second ridge is less clearly defined. Between the two ridges cilia beat transversely away from the mid-ventral line, and so material entering the stomach from the oesophagus is carried to the anterior roof of the stomach, either to a group of isolated ducts from the digestive diverticula (DDD) on the right side, or to the dorsal hood.

The style-sac (SS) and mid-gut (MG) are conjoined and pass downwards from the posterior floor of the stomach. The minor typhlosole is bulbous, and terminates at the mouth of the mid-gut. The major typhlosole (TY) forms a broad horizontal shelf which arches widely over the intestinal groove (IG). The major typhlosole, accompanied throughout its course by the intestinal groove, passes forwards over the floor of the stomach and passes into the right caecum (RC). Very powerful ciliary currents sweep forwards over the upper surface of the major typhlosole. The right caecum passes deeply beneath the stomach, and receives seven large and two small ducts from the digestive diverticula. The major typhlosole penetrates the right caecum to its apex, and sends small flares into the mouths of all the large ducts. The major typhlosole emerges from the right caecum on its anterior side and passes transversely across the anterior floor of the stomach, here forming a large forwardly projecting flap with a flat anterior side, which is pressed forwards over the intestinal groove, towards the orifice of the oesophagus. The major typhlosole then enters the left caecum (LC), which it penetrates very deeply, finally terminating at the mouth of the left caecum, on its posterior side. Seven large ducts enter the left caecum from the digestive diverticula, and flares pass into their mouths from the border of the major typhlosole. The intestinal groove originates (OIG) as a slight groove on the left anterior floor of the stomach, which leads into the left caecum.

The left pouch (LP) is very well developed, and lies on the left anterior wall of the stomach, above the orifice of the left caecum, and anterior to that of the dorsal hood. It curves backwards beneath the dorsal hood, and receives one large and three small ducts from the digestive diverticula. A sorting area (SA^6) of fine ridges and grooves emerges on to the floor of the stomach from

the left pouch, and ciliary currents on this sorting area pass backwards in the grooves towards the gastric shield.

The dorsal hood (DH) is very well developed. Its anterior, or ventral, wall bears a broad smooth ridge adjacent to the margin of the gastric shield, and then a broad sorting area (SA^3) of finely disposed transverse ridges and grooves, which passes out of the dorsal hood and expands widely over the right posterior wall of the stomach. The posterior limits of this sorting area come close to the mouth of the mid-gut, and here the sorting area passes into a shallow, blind pocket (B). Cilia on the crests of the ridges on this sorting

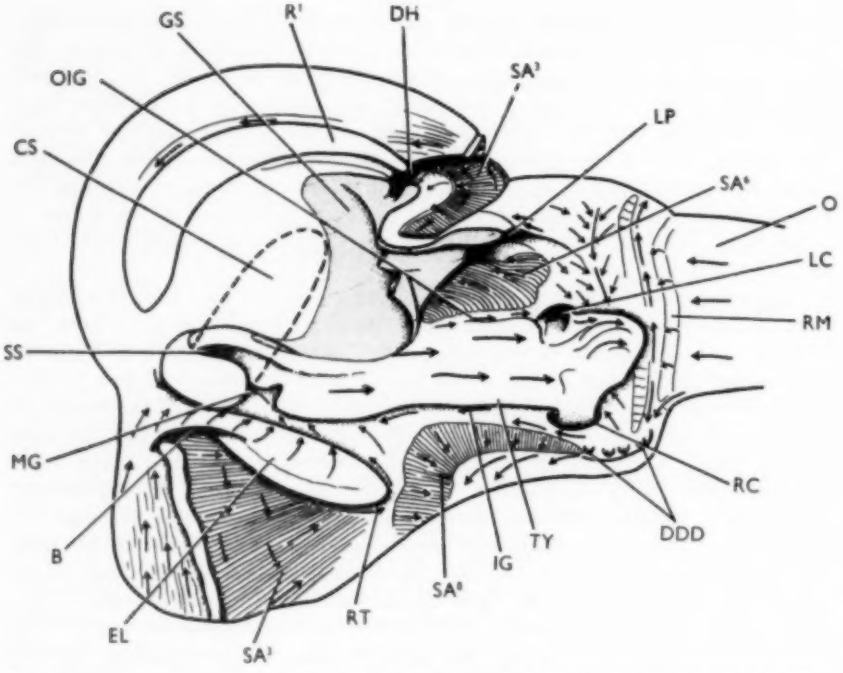

Fig. 9.—*Glauconome rugosa*. Interior of the stomach after opening by a mid-dorsal incision. (For lettering see p. 487.)

area beat transversely over the ridges, up the right side of the stomach and towards the apex of the dorsal hood. Cilia in the grooves beat along the grooves, downwards and into a rejection tract (RT) that discharges material into the intestinal groove. The lower border of this sorting area is separated from the intestinal groove by a broad forwardly projecting tongue (EL) over which cilia beat strongly towards the intestinal groove.

Ciliary currents on the roof of the dorsal hood pass out of the dorsal hood and on to the posterior wall of the stomach. There is a broad ridge (R^1) on the posterior wall.

The gastric shield (GS) lies in the middle of the left side of the stomach, and sends well-defined flares into the mouths of the dorsal hood and of the left pouch.

There is an additional sorting area (SA^8) on the right anterior wall of the stomach. This consists of a belt of finely disposed transverse striations, which passes backwards from the right border of the orifice of the oesophagus, along the right side of the stomach, and finally over the roof of the stomach towards the dorsal hood. Cilia in the grooves of this sorting area beat forwards along the grooves and into a ciliary tract that leads into the dorsal hood. At the anterior end of this sorting area, close to the oesophageal orifice, and dorsal to the mouth of the right caecum, there is a group of four isolated orifices of ducts from the digestive diverticula (DDD).

Owen (1959) showed that the generic name *Glauconome* Gray (1828) should replace *Glaucomya* Bronn (1838), and gave evidence for exclusion of the Glaucomyidae from the Solenacea. He concluded that the Glaucomyidae should be placed in the Veneracea.

Petricolidae

Petricola pholadiformis Lam.

The internal structure and the function of the stomach of *P. pholadiformis* have been adequately figured and described by Purchon (1955 a) and no further information can yet be added to that account.

Lucinopsis (*Mysia*) *undata* (Pennant)

The structure of the stomach of *L. undata* is almost identical with that of *Gafrarium minimum* (see above), save that the stomach of *Lucinopsis* is considerably larger and that the upper lobe of the right caecum receives only one duct from the digestive diverticula on its anterior wall, and the lower lobe of the right caecum receives about six ducts from the digestive diverticula. The tongue of the major typhlosole which projects into the right caecum is longer in *Lucinopsis* than in *Gafrarium*, while the lobe on the floor of the mouth of the left pouch is globular and very large in *Lucinopsis*.

MACTRACEA

Mactridae

Mactra mera Reeve (Fig. 10)

The stomach lies antero-dorsally in the visceral mass close to the epithelium, and is easily separated from the branches of the gonad which cover its posterior half. The oesophagus lies almost horizontally and enters the anterior face of the stomach. The style-sac (SS) is wholly separate from the mid-gut, and passes obliquely downwards and backwards from the posterior floor of the stomach. The mid-gut (MG) leaves the stomach a little further forward on its right side, and passes back into the visceral mass, parallel with the style-sac. The digestive diverticula form a compact golden brown mass on the anterior side of the stomach and surrounding the upper part of the mid-gut. The

walls of the stomach are very thin and transparent, and the two sorting areas that pass out of the dorsal hood and over the right wall of the stomach can be seen by transparency before opening the stomach.

The orifice of the oesophagus (O) into the stomach is " D "-shaped, its upper border being straight, and the remainder being semi-circular. The orifice is surrounded by a series of large fleshy papillae (PR) the upper borders of each of these bearing a double series of beads. There are about four such papillae above the oesophageal orifice, while about eight more are arranged round the sides and lower border of the orifice. Smaller papillae alternate between the bases of the larger papillae, and a series of minute beads surrounds the orifice at the bases of the papillae.

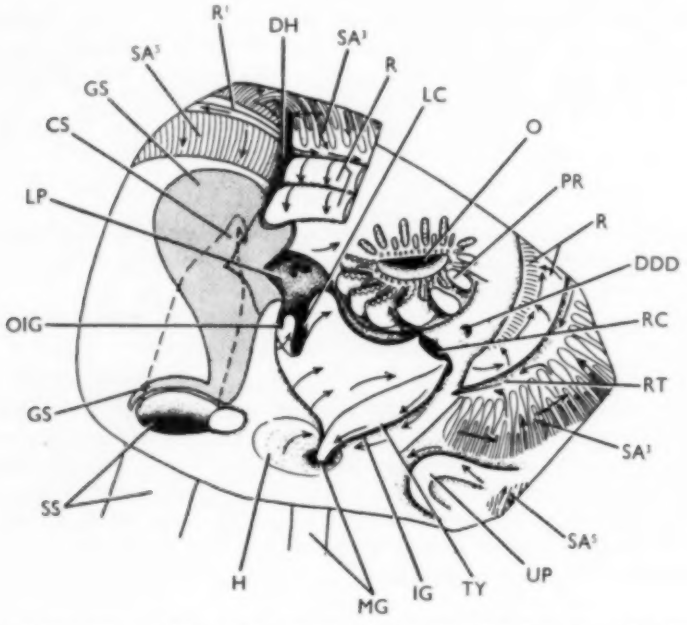

Fig. 10.—*Mactra mera*. Interior of the stomach after dissection from the right side. (For lettering see p. 487.)

As mentioned above, the style-sac is completely separate from the mid-gut, and a globular swelling on the anterior border of the former may possibly indicate the point of fusion. There is no minor intestinal typhlosole. The major typhlosole (TY) is large and cylindrical within the mid-gut. Where it enters the stomach it gradually flattens, and passes forwards over the floor of the stomach, accompanied throughout its course by the intestinal groove (IG). It enters the right caecum (RC), penetrating it very deeply with a semi-circular flare. Numerous ducts from the digestive diverticula open in groups of three or four into pockets in the walls of the right caecum, and a frill of the major typhlosole projects into each of these pockets. A single duct from

the digestive diverticula opens into the stomach independently on the right wall, above the mouth of the right caecum (DDD).

The major typhlosole crosses the anterior floor of the stomach and enters the left caecum (LC) on its anterior side. It penetrates the left caecum deeply with a semi-circular flare, terminating on the posterior border of the mouth of the left caecum. The origin of the intestinal groove (OIG) thus lies at the mouth of the left pouch. The number of ducts from the digestive diverticula, and their relations with the major typhlosole are the same as in the right caecum.

The dorsal hood (DH) is very well developed. It arises from the roof of the stomach and curves forwards and to the left. Its anterior wall bears two thick ridges (R) which pass over to the right side of the stomach, and terminate above and behind the mouth of the right caecum. The lowermost of these ridges bears a series of short transverse striations. Above these two ridges, the anterior face of the dorsal hood bears an extensive sorting area (SA^3) of transverse ridges and grooves, of which approximately every fourth ridge is longer than the remainder and terminates in a bulbous swelling. This sorting area extends over the roof and on to the right side of the stomach. It is bordered on its anterior side by a rejection tract (RT) which passes material into the intestinal groove. On the crests of the folds of this sorting area cilia beat transversely, over the crests and towards the apex of the dorsal hood. In the grooves between the ridges the cilia beat along the grooves and into the rejection tract.

There is a sorting area (SA^5) on the posterior wall of the dorsal hood, consisting of a narrow belt of finely disposed transverse ridges over which cilia beat downwards along the ridges towards the gastric shield. This sorting area terminates on the right side of the stomach and below its termination there is a conspicuous downward projecting swelling (UP) which under natural conditions tends to arch over the intestinal groove and touch the major typhlosole. The two sorting areas of the dorsal hood are separated from each other by a longitudinal ridge (R^1) along which cilia beat out of the dorsal hood towards the posterior wall of the stomach.

The left pouch (LP) lies in front of, and below the mouth of the dorsal hood, beneath which it penetrates deeply. Five ducts enter the left pouch from the digestive diverticula, two of these opening on its left side, and three opening near its apex. There are no sorting areas within the left pouch.

The gastric shield (GS) lies on the left side of the stomach, but does not protect the posterior wall, from which it seems to have retreated. The gastric shield provides a very firm sheath to the pillar which forms the posterior border of the mouth of the left pouch and the anterior border of that of the dorsal hood. A long, firm and relatively slender tongue of the gastric shield passes far into the left pouch, on its posterior side. A saddle-shaped lobe of the gastric shield invests the lower border of the mouth of the dorsal hood, the posterior part of this lobe being relatively thin. A stiff downward prolongation of the gastric shield reaches the anterior border of the mouth of the style-sac and sends a stiff sickle-shaped projection backwards around the median side of the mouth of the style-sac.

A semi-circular hollow (H) surrounds the mouth of the mid-gut.

Mesodesmatidae

Atactodea glabrata Lamarck (Fig. 11)

The stomach is large and irregular in shape. The oesophagus, which is comparatively slender, opens on the anterior face of the stomach (O). The style-sac (SS), which is completely separate from the mid-gut, passes vertically downwards from the postero-ventral wall of the stomach. There is a large globular swelling on the left anterior border of the orifice of the style-sac, and this swelling passes forwards into a ridge which runs anteriorly over the floor of the stomach. The crystalline style projects vertically upwards into the stomach, and its tip enters the mouth of the dorsal hood. The mid-gut (MG) opens on the right anterior floor of the stomach, some distance away from the orifice of the style-sac, with which it has no connection. There is no minor typhlosole.

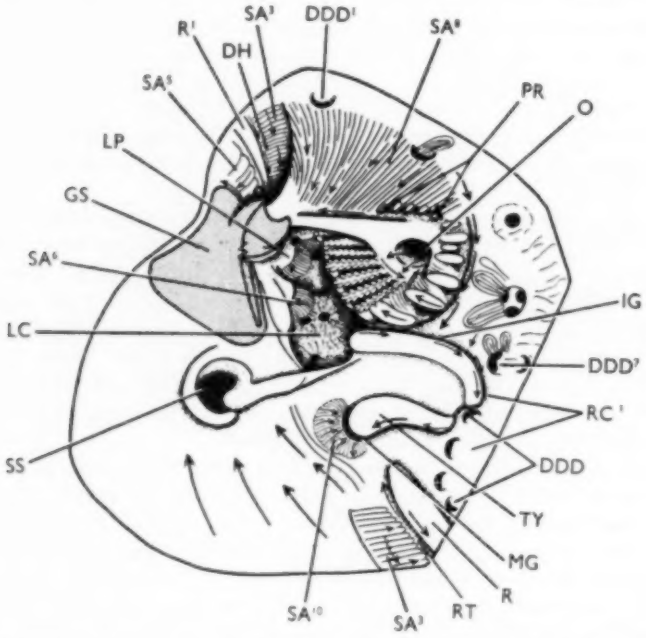

Fig. 11.—*Atactodea glabrata*. Interior of the stomach after opening by an oblique incision in the right side. Note that the right caecum (RC^1) has been dissected open. × 15. (For lettering see p. 487.)

The major typhlosole is greatly swollen within the mid-gut, and is even more inflated just within the stomach. The major typhlosole (TY), accompanied throughout its course by the intestinal groove (IG), passes forwards and to the right and enters the mouth of a broad and shallow right caecum (RC^1) within which it forms a semi-circle before emerging on the anterior side of the right caecum. The major typhlosole then passes transversely to the left

across the anterior floor of the stomach and passes downwards into a very extensive left caecum (LC), the mouth of which lies on the left anterior floor of the stomach. The major typhlosole forms a loose spiral of about two and a half turns on the median and posterior wall of the left caecum, and terminates on its posterior wall near its orifice.

The dorsal hood (DH) lies on the postero-dorsal wall of the stomach, and is relatively small. On its anterior wall there is an extensive sorting area (SA^8) of ridges and grooves, which passes forwards over the roof of the stomach towards the right side of the oesophageal orifice. Cilia beat downwards in the grooves of this sorting area, while an acceptance tract passes from right to left along the anterior border of the sorting area, conveying material into the dorsal hood. This acceptance tract is bordered anteriorly by a well-defined ridge which passes backwards from the left border of the oesophagus to the mouth of the dorsal hood. The last five ridges on the right-hand side of this sorting area terminate anteriorly in small papillae (PR), which are graded in size, increasing gradually towards the right-hand side of the oesophageal orifice, and grading imperceptibly into a series of papillae of considerable size and complexity which lie on the right side of the oesophageal orifice, and ventrally between it and the transverse part of the intestinal groove. There are about twenty such papillae, and each bears a double series of lobes on its upper border. Dorsalward ciliary currents occur on the smooth posterior sides of these papillae, and a ciliary current passes from left to right along the anterior side of the bases of the papillae. The papillae exhibit considerable muscular activity. A similar series of papillae was found in the same position in the stomachs of large specimens of *Pholadidea loscombiana* (Purchon, 1955) and also in *Mactra mera* and in *Caecella cumingiana*, described in this paper.

There is a sorting area (SA^3) on the roof of the dorsal hood, on which cilia beat over the crests of the folds towards the apex of the dorsal hood. Cilia beat anteriorly in the grooves between the folds, into a rejection tract (RT). This sorting area and the accompanying rejection tract extend on to the right side of the stomach, and the rejection tract discharges material into the intestinal groove. The rejection tract is separated from the posterior border of the right caecum by a well-defined ridge (R). On the posterior wall of the dorsal hood there is a small sorting area (SA^5) of relatively large folds, on which cilia beat downwards and out of the dorsal hood, and a longitudinal ridge (R^1).

The left pouch (LP) lies on the left anterior wall of the stomach, between the mouths of the left caecum and of the dorsal hood. There is no line of demarcation between the left caecum and the left pouch. About fourteen ducts enter the left caecum, and about eight ducts enter the left pouch, from the digestive diverticula on the left and left-anterior sides of the stomach. The lateral wall of the left caecum and floor of the left pouch are covered by a contorted system of ridges and grooves. In addition, a narrow belt of fine transverse ridges and grooves (SA^6) arises on the floor of the left pouch, penetrates to the apex of the left pouch, and then passes on to its roof. On this sorting area the cilia beat posteriorwards in the grooves.

About seven ducts from the digestive diverticula open into the stomach in a scattered series (DDD^1–DDD^7) along the posterior border of the sorting

area on the roof (SA^8). Four ducts from the digestive diverticula open into the broad and shallow right caecum (DDD).

The gastric shield (GS) is large and firm, and sends a deeply saddle-shaped flare into the mouth of the dorsal hood, and it also invests the posterior border of the left pouch.

There is a small sorting area (SA^{10}) of fine radiating ridges and grooves on the posterior border of the orifice of the mid-gut. Ciliary currents in the grooves beat along the grooves and into the mid-gut.

Caecella cumingiana Deshayes (Fig. 12)

Specimens of *C. cumingiana* were found in abundance in drifts of coarse sand just within the margin of an area of mangrove at Kranji, on the Singapore coast of the Straits of Johore. These patches of sand were at or above mean sea level, were well drained, and were shaded by the mangrove plants. The bivalve was sufficiently abundant to be collected from the sand by hand.

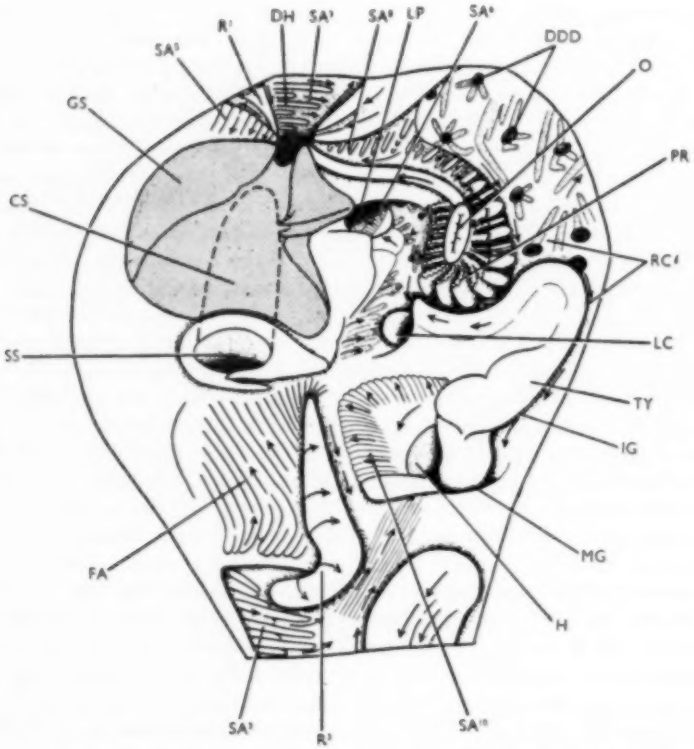

Fig. 12.—*Caecella cumingiana*. Interior of the stomach after opening by an oblique incision in the right side. Note that the right caecum (RC^1) has been dissected open. (For lettering see p. 487.)

The description of the stomach of *Atactodea glabrata*, given above, applies equally well to that of *C. cumingiana* except for the following minor details. The major typhlosole (TY) does not form a spiral of two and a half turns, but is semi-circular in shape within the left caecum. The principal sorting area of the dorsal hood (SA^3) spreads out more widely on the right side of the stomach, and discharges into the mid-gut via an area of wrinkles lying in a defile between two conspicuous ridges. A conspicuous ridge (R^3) passes down the right side of the stomach from the lower border of the sorting area (SA^3) towards the mouth of the style sac. An area of regular folds (FA) which does not appear to act as a sorting area, lies on the posterior floor of the stomach. Ciliary currents on this folded area beat along the grooves towards the mouth of the style sac. The ridge which passes from the mouth of the dorsal hood along the ventral border of the sorting area (SA^8) does not join the left, but the right corner of the oesophageal orifice. In the series of large papillae which lie below the oesophageal orifice, alternate members were very deeply bifid.

TELLINACEA

Tellinidae

Tellina crassa Pennant

T. tenuis da Costa

Graham (1949) has figured and described the interior of the stomach of *T. crassa*, and it is clear that it is of Stomach Type V. The main structural features of interest are as follows : The stylei-sac and mid-gut are conjoined ; three ducts enter the right caecum from the digestive diverticula, while eight enter the left caecum and one duct opens ndependently on the right wall, above the mouth of the right caecum.

Graham states that the intestinal groove runs along the whole length of the major typhlosole, and it should therefore terminate at the centre of the spiral of the typhlosole in the left caecum. It is not clear on what grounds Graham states that the intestinal groove ends at the mouth of the left caecum.

The only sorting area which is shown in Graham's Fig. 9 is that lying on the floor of the mouth of the left pouch ($=SA^6$). Graham states that the " posterior sorting area " is present, though only slightly developed, but the position of this sorting area (Graham, 1949, Fig. 9, SAP) is on the posterior wall of the stomach close to the gastric shield, and far removed from the intestinal groove. It is therefore difficult to accept this as equivalent to the " posterior sorting area " described by Graham in other genera.

Yonge (1949) figured and described an appendix in *Tellina tenuis*, under the name " postero-dorsal caecum ".

Tellina capsoides Lamarck

A few specimens were obtained from the sandy bed of a shallow river draining an area of mangrove and opening into the Straits of Johore.

Examination of the stomachs showed that four ducts from the digestive diverticula opened into the left pouch, six ducts entered the left caecum and

four ducts entered the right caecum. No ducts opened independently into the stomach. The major typhlosole and the accompanying intestinal groove formed an even spiral of two and a half turns on the anterior face of the left caecum. A sorting area (SA^6) extended up the left side of the left caecum and into the mouth of the left pouch, and a sorting area (the same ?) passed out of the left pouch on its upper rim and entered the mouth of the dorsal hood on its anterior face. There was a small sorting area (SA^5) on the posterior wall of the dorsal hood. The appendix was remarkable in possessing four lobes of approximately equal size. In all other respects there is correspondence with the account given above for *T. crassa* and *T. tenuis*.

Psammobiidae

Solecurtus chamasolen (da Costa)

Graham (1949) has figured and described the interior of the stomach of *S. chamasolen*, which is clearly of Stomach Type V. The following anatomical features are worthy of mention : The style-sac and mid-gut are conjoined ; a single duct from the digestive diverticula enters the stomach independently on its right side, and from this point two adjacent ridges pass up the right wall of the stomach and enter the dorsal hood ; Graham shows a well-developed sorting area on the anterior face of the stomach (=SA^7), between the orifice of the oesophagus and the transverse part of the intestinal groove, but no ciliary action is indicated on the figure (Graham's Fig. 13), nor is this sorting area mentioned in the text ; Graham states that the " posterior sorting area " is relatively small in *Solecurtus*, and its position is marked in the figure (Graham's Fig. 13, SAP), but the folds of the sorting area are not actually drawn.

Gari togata Deshayes (Fig. 13)

The stomach lies dorsally, close to the hinge line, and is surrounded laterally and ventrally by a thick layer of dark green digestive diverticula. The oesophagus (O) enters the stomach antero-dorsally, its orifice into the stomach being marked ventrally by a transverse lobed ridge (RM) which is capable of muscular movement. The combined style-sac (SS) and mid-gut (MG) leaves the postero-ventral wall of the stomach. The minor intestinal typhlosole terminates at the mouth of the mid-gut.

The major typhlosole is unusual in form, consisting of two distinct parts. There is a stiff, raised semi-circular elevation (E), the upper surface of which shows no ciliary activity, which curves to the left over the floor of the stomach in much the same way as has been described for the major typhlosole in Stomach Type IV (Purchon, 1958). Under the margin of this shelf cilia beat strongly towards the orifice of the left caecum (LC) so this ridge, being unaccompanied by an extension of the intestinal groove, cannot be regarded as the major typhlosole proper. The second part of the major typhlosole (TY) arises in the mouth of the mid-gut (MG), and passes forwards over the floor of the stomach, accompanied throughout its course by the intestinal groove. The

major typhlosole sends a short semi-circular flare into the right caecum (RC), into which open a number of ducts from the digestive diverticula. The major typhlosole passes out of the right caecum and transversely across the anterior floor of the stomach to enter the left caecum (LC), which receives eight ducts from the digestive diverticula, the mouths of two of these ducts receiving flares from the major typhlosole.

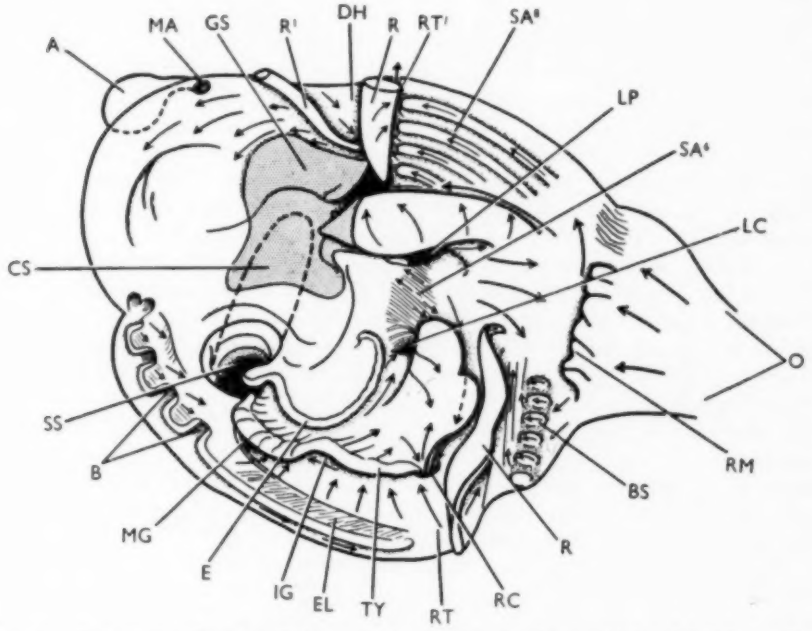

Fig. 13.—*Gari togata*. Interior of the stomach after opening by a mid-dorsal incision. (For lettering see p. 487.)

The major typhlosole penetrates to the apex of the left caecum, turns and terminates in a loose and incomplete spiral about half way back towards the orifice of the left caecum.

The dorsal hood (DH) is large and well defined, the lower border of its orifice being protected by a very stiff saddle-shaped sheath of the gastric shield (GS). A broad ridge (R) enters the dorsal hood on the anterior side of its roof, while a more slender ridge (R^1) lies on the posterior side of the roof. Between these two ridges there is a ciliated area on which material is driven downwards, to the apex of the dorsal hood. Posterior to the slender ridge (R^1) cilia beat backwards, out of the dorsal hood and towards the orifice of the appendix (MA). The appendix (A) is large and well defined, in the form of a very distensible pear-shaped chamber which opens into the stomach by a slender, smooth walled neck. A few sand grains were found in the appendix.

The left pouch (LP) lies antero-ventral to the mouth of the dorsal hood, the posterior border of its mouth being protected by a stiff, saddle-shaped

flare of the gastric shield. The left pouch passes backwards under the dorsal hood, the two being of comparable size. About six ducts enter the left pouch from the digestive diverticula on the left side of the body.

The sorting areas of the stomach are few in number. On the anterior side of the dorsal hood there is a sorting area (SA^8) consisting of about four large and well-spaced ridges. On the left border of this sorting area an acceptance tract conveys material from the left margin of the oesophageal orifice, backwards into the dorsal hood. On the posterior border of the sorting area, and adjacent to the broad ridge (R) on the roof of the dorsal hood, there is a rejection tract (RT) which conveys material transversely over the roof of the stomach and down its right side posterior to the mouth of the right caecum and into the intestinal groove (IG). The lower border of this sorting area lies on the right side of the stomach, where a long forward-projecting tongue (EL) separates the sorting area from the intestinal groove. The postero-ventral border of this sorting area, close to the mouth of the style-sac and mid-gut, is marked by a series of five or six shallow blind pockets (B).

A sorting area of extremely fine striations (SA^6) lies on the left anterior floor of the stomach, and extends into both the left caecum and the left pouch. Particles which are directed forwards along the ridges of this sorting area do not enter the left caecum, but are passed into the intestinal groove.

In the mouth of the right caecum (RC) cilia on the posterior part of the upper surface of the major typhlosole beat strongly inwards, while anteriorly the cilia beat strongly out of the right caecum. It is difficult to determine the action of these currents under normal conditions, but it is possible that some of the particles will be carried into the right caecum, deposited there and carried thence to the digestive diverticula, while the orifice of the right caecum itself will be kept free from depositions.

The orifice of the right caecum is protected against the entry of material from the oesophagus by a broad delicate flap (R) which extends up the right wall into the dorsal hood, and in front of which there is a series of six bead-like swellings (BS), and an ill-defined system of grooves on which material is diverted towards the centre of the floor of the stomach.

The specimens were dissected after remaining for one day in an aquarium. The crystalline style (CS) projected far into the stomach, and was of a dirty brown colour, due perhaps to the incorporation into its substance of material lying in the adjacent mid-gut. The style was firm, and there was no reason to believe other than that the contents of the stomach were normal in every way. The stomach was filled with a very sticky greenish material that extended into all corners of the stomach. A greenish sticky cord lying in the intestinal groove was independent of the mass filling the stomach. Rotation of the crystalline style will cause the sticky stomach contents to be wound round the head of the style like a capstan, and the peripheral material will be brushed against the ciliary sorting areas in the vicinity of the dorsal hood, as described by Owen (1953). It seems improable that individual particles could be torn out of this extremely viscous mass and, if this is the normal condition of the stomach contents, the ciliary surfaces of the stomach are not likely to be concerned in the manipulation of individual particles. The

paucity and simplicity of the sorting areas of the stomach in *G. togata* may perhaps be correlated with the unusually high viscosity of the stomach contents.

Asaphis deflorata L. (Fig. 14)

The dark brown digestive diverticula lie on the anterior side of the stomach in a vertical mass from which two horns pass backwards, one over the top of the stomach and the other ventrally under the hind-gut. They are closely packed, but can be divided into three parts, left and right dorsal parts which enter the left pouch and right caecum respectively, and a ventral lobe which enters the left caecum.

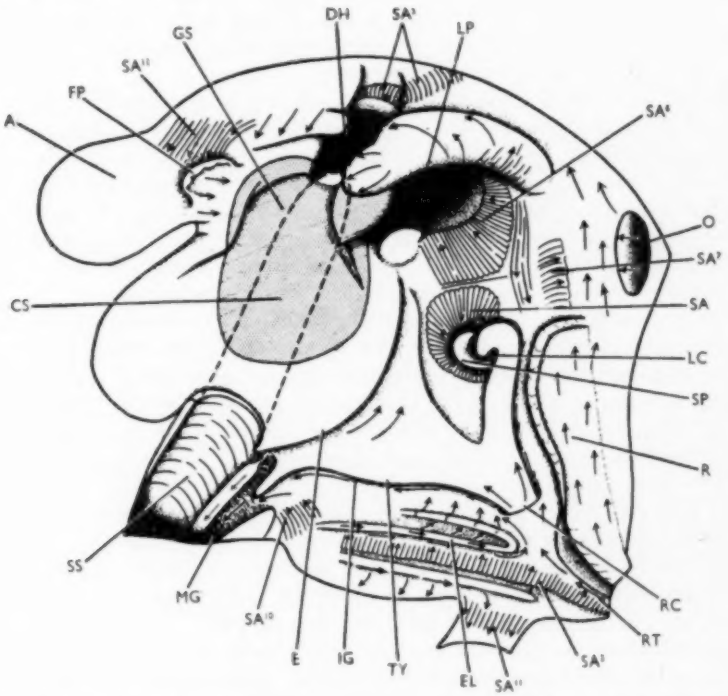

Fig. 14.—*Asaphis deflorata*. Interior of the stomach after opening by a mid-dorsal incision from the oesophagus to the mid-gut. (For lettering see p. 487.)

The oesophagus (O) enters the stomach antero-dorsally and the combined style-sac (SS) and mid-gut (MG) leaves the postero-ventral floor of the stomach. It is worthy of mention that the proximal end of the hind-gut consists of an extra-ordinary dilatation nearly half an inch in diameter, and about three-quarters of an inch long in a fully grown animal. This dilatation is tightly filled with a cylindrical compacted faecal mass, bound together with mucus. The mid-gut enters dorsally and the hind-gut leaves it ventrally. The purpose served by this remarkable arrangement for the retention of faeces is not known.

On emerging from the mid-gut into the stomach, the major typhlosole divides into two parts. The posterior of these is a relatively stiff semi-circular elevation (E) which runs across the floor of the stomach to terminate outside the mouth of the left pouch (LP). The anterior part is typical in running forwards, accompanied throughout its course by the intestinal groove (IG) on its right side. It sends a short semi-circular tongue into the right caecum (RC) and then passes transversely across the anterior floor of the stomach to the mouth of the left caecum (LC), which here occupies a ventral position. The major typhlosole enters the left caecum on its anterior side, and forms a loose spiral on its median and posterior wall, terminating centrally. A portion of this spiral may be seen at the mouth of the left caecum (Fig. 14, SP). The wall of the left caecum bears a sorting area (SA) of finely disposed ridges and grooves which radiate towards the intestinal groove, into which the sorting area discharges material by ciliary action.

The dorsal hood (DH) is short and broad and curls backwards and to the left over the roof of the stomach. The ventral border of its mouth is invested by a saddle-shaped lobe of the gastric shield (GS). A thick ridge passes backwards from the left anterior wall of the stomach and enters the dorsal hood low down on its anterior face. Dorsal to this ridge there is a sorting area (SA^3) of fine transverse folds on the anterior face, or roof, of the dorsal hood. On the smooth posterior wall of the dorsal hood ciliary currents pass backwards, and convey material towards the mouth of the appendix (A).

The appendix is a capacious sac, the walls of which are capable of considerable muscular action, which lies on the postero-dorsal side of the stomach. Its opening into the stomach is guarded by two large fleshy pads, of which only one is shown in the figure (FP). There are sorting areas (SA^{11}) of irregularly parallel folds on the left and right sides of the mouth of the appendix, and ciliary currents on these sorting areas beat inwards, passing material into the appendix from the mouth of the dorsal hood and from the right posterior wall of the stomach. No outward ciliary currents were found, and it is possible that the contents of the appendix are discharged into the stomach by muscular contraction of its walls. In one of the specimens dissected the contents of the appendix included a number of relatively large objects, including sand grains, organic débris, bits of alga, and an egg (fish?).

The left pouch (LP) lies anterior and ventral to the dorsal hood, the posterior border of its wide mouth being protected by a flare from the gastric shield (GS). The left pouch is of considerable size, and passes backwards under the dorsal hood, receiving about twelve ducts from the digestive diverticula. There is a well-developed sorting area (SA^6), of finely disposed ridges and grooves, on the floor of the left pouch at its mouth. Here cilia beat along the ridges and into the left pouch. Within the left pouch there are two further sorting areas, on which the cilia beat along the ridges and away from the mouths of the ducts from the digestive diverticula.

There is a long narrow sorting area (SA^3) on the right side of the stomach and extending over its roof and into the dorsal hood. The posterior part of this sorting area is bounded dorsally and ventrally by a pair of long slender ridges ; the ventral tongue (EL), which lies between the sorting area and the

intestinal groove (IG), arises near the mouth of the mid-gut, and is "U" shaped. On the sorting area cilia beat forwards and downwards in the grooves, and into a rejection tract (RT) which passes out of the dorsal hood, down the right side of the stomach anterior to the sorting area, and discharges into the intestinal groove immediately behind the mouth of the right caecum (RC). It is by no means impossible that some of the material in this rejection tract may enter the right caecum. A small sorting area (SA^{10}) lies close to the mouth of the mid-gut, into which it directs particles by ciliary action.

On the anterior floor of the stomach there is a broad fleshy transverse flap (R), which arises near the median line between the oesophageal orifice and that of the left caecum. This flap passes across the stomach to the right, in front of the transverse part of the intestinal groove and the mouth of the right caecum, up the right wall of the stomach and on to its roof, where it terminates. Ciliary currents on the anterior side of this flap are slow to start, but when initiated they carry material from right to left, and deliver it to the mouth of the left pouch. This flap will protect the intestinal groove and right caecum, preventing material from passing directly thither from the orifice of the oesophagus.

There is a weakly developed anterior sorting area (SA^{7}) on the anterior floor of the stomach, immediately below the opening of the oesophagus.

Semelidae

Abra alba (Wood)

Scrobicularia plana (da Costa)

Yonge (1949) compared the structure of these two species with that of *Tellina tenuis*, which he studied and described in greater detail. The present writer has also very briefly examined the stomach of *S. plana* (Purchon, 1955). These old accounts do not contain the detailed information that is desirable for the present survey, and the only certain information is that the style-sac and mid-gut are conjoined. In view of the surprising occurrence of a stomach of type IV in *Donax faba* it is not even safe to assume that these two genera resemble *Tellina* in possessing a stomach of type V.

SOLENACEA

Solenidae

Pharella acutidens (Broderip & Sowerby) (Fig. 15)

The stomach is elongated, with a horizontal long axis. Its dorsal, anterior and ventral walls are largely covered with a dense mass of dark green digestive diverticula, and the posterior part of the sides of the stomach are thinly covered with acini of the gonad. The broad and dorso-ventrally flattened oesophagus passes backwards and slightly upwards to open into the stomach on its anterior face (O), the orifice bearing protuberant dorsal and ventral lips. The style-sac (SS) and mid-gut (MG) are separate, and leave the posterior floor of the stomach. The mid-gut opens in front of, and a little to the right of the orifice of the style-sac. The major typhlosole is a swollen cylinder

within the mid-gut, but is constricted slightly at the mouth of the mid-gut. Within the stomach it becomes flattened (TY) to form a very broad and flimsy roof to the accompanying intestinal groove (IG). The major typhlosole passes into the right caecum (RC), within which it forms an extensive semicircular tongue with a very frilly margin. The major typhlosole emerges from the right caecum close to the median line, crosses the anterior floor of the stomach and plunges almost immediately into the left caecum (LC) in which

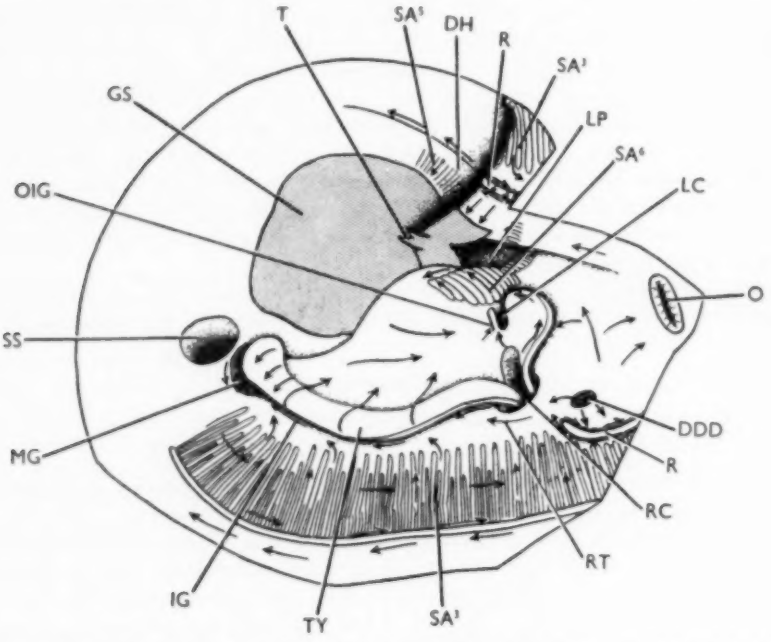

Fig. 15.—*Pharella acutidens.* Interior of the stomach after opening by a mid-dorsal incision. × 8 approx. (For lettering see p. 487.)

it forms an equally extensive semicircular tongue. The major typhlosole emerges from the left caecum on its posterior side, and the origin of the intestinal groove (OIG) lies on the anterior floor of the stomach, close to the median line.

Numerous ducts from the digestive diverticula open into the right and the left caeca, but it was not possible to estimate their number since the walls of the caeca are very thin and the ducts sub-divide soon after leaving the caeca. In addition two ducts open independently into the stomach by a single aperture (DDD) on the right side of the stomach, above the mouth of the right caecum.

The left pouch (LP) lies on the left anterior wall of the stomach, in front of and below the mouth of the dorsal hood. It passes far backwards horizontally below the dorsal hood and receives a series of five small ducts from the digestive

diverticula along its outer wall. A slender sorting area of transverse ridges and grooves extends along the outer wall of the left pouch, and passes over its floor on to a conspicuous oval swelling (SA^6) which projects on to the floor of the stomach.

The dorsal hood (DH) is very well developed. It is dorso-ventrally compressed and curves to the left and then backwards close to the left side of the stomach. The anterior, or ventral, wall of the dorsal hood bears a well-developed sorting area (SA^3) of alternate long and short ridges. This sorting area extends over the roof of the stomach and far backwards over the right side of the stomach. A slender ridge (R) arises on the right side of the stomach, just behind and above the mouth of the independent group of ducts from the digestive diverticula. The ridge passes over the roof of the stomach and into the dorsal hood alongside the sorting area. On the anterior, or ventral side of this ridge cilia beat along the ridge and into the dorsal hood, while on the opposite side of the ridge there is a rejection tract (RT) which beats in the opposite direction and discharges material from the dorsal hood into the intestinal groove. Cilia on the ridge beat transversely over the ridge from the rejection tract towards the ciliary current that is directed into the dorsal hood. On the posterior wall of the dorsal hood there is a broad ridge which bears a very fine sorting area (SA^5). On the upper border of this ridge there is a ciliary current which carries material out of the dorsal hood and on to the posterior wall of the stomach.

The gastric shield (GS) covers the left side and floor of the stomach. It sends two very long, slender, gutter-shaped prolongations, one into the dorsal hood and the other, which is even longer, into the left pouch.

As was found in the case of *Gari togata*, the stomach contents were very viscous and strands were wound round the head of the crystalline style and extended across the stomach to the left caecum, and to the orifice of the oesophagus.

Ensis siliqua (Schumacher)

Graham (1949), having referred to his own earlier work and to other relevant literature, redescribed and figured the interior of the stomach of *E. siliqua*, which corresponds closely with that of *Pharella acutidens* given above.

With reference to Graham's Fig. 15, the present writer agrees with Owen (1959) that the dorsal hood is not the small and inconspicuous hollow (P) adjacent to the gastric shield, but is the large and well-developed backwardly-directed horn (SAPC), into which Graham's " posterior sorting area " extends. On this interpretation, the stomach of *Ensis* corresponds in structure with the stomachs of a very large number of genera described in the present survey, and it is by no means clear why Graham should have thought otherwise.

MYACEA

Myidae

Mya arenaria L. (Fig. 16)

Yonge (1923) studied the interior of the stomach of *Mya* and stated that the digestive diverticula open into it by three asymmetrically placed orifices.

These can now be interpreted as the left pouch, the left caecum and the right caecum. Later (1946) he erroneously stated that there were two openings from the digestive diverticula into the stomach in *Mya*.

The stomach is large and thin walled, and lies above and behind a compact mass of digestive diverticula. The oesophagus enters the stomach antero-dorsally, its inner walls being very deeply folded longitudinally (O), and its orifice into the stomach being marked by a fleshy lobed rim (RM). The style-sac (SS) and mid-gut are separate, the style-sac leaving the posterior end

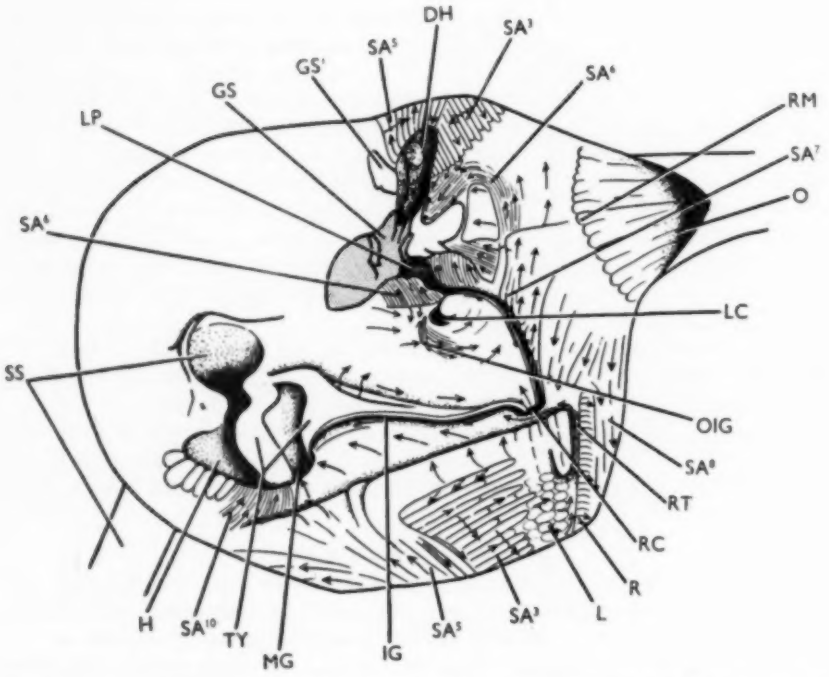

Fig. 16.—*Mya arenaria*. Interior of the stomach after opening by a mid-dorsal incision. (For lettering see p. 487.)

of the stomach and passing obliquely downwards and backwards into the visceral mass, while the mid-gut (MG) arises on the right side of the style-sac and passes downwards and forwards into the visceral mass, tapering gradually on its course. There is a hemispheric pocket (H) at the mouth of the mid-gut, on the posterior side of the major typhlosole, and this communicates on its left side with the lumen of the style-sac, as the rim between the two is low at one point. On the right side, this hemispheric pocket communicates with the lumen of the mid-gut. No ciliary action was observed in this pocket, but particles falling here were quickly bound into a sheet with mucus.

In the mouth of the mid-gut the major typhlosole (TY) is greatly swollen, effectively separating the mid-gut from the style-sac. The major typhlosole is unusual in that there is a break in its structure at the mouth of the mid-gut, and a separate major typhlosole (TY) arises here and passes forwards into the stomach, accompanied throughout its course in the usual manner by the intestinal groove (IG). The two structures pass forwards over the floor of the stomach, and pass into the right caecum (RC). The right caecum has a very wide mouth, and receives a large number of ducts from the digestive diverticula. It was difficult to count these, for they are complex, and subdivide almost immediately. Nevertheless it was estimated that about twelve ducts from the digestive diverticula open here, and frills on the border of the major typhlosole pass into the mouths of these ducts. In the mouth of the right caecum there is a steady outward ciliary current over the greater part of the surface of the major typhlosole, there being a small inward current only at the posterior border of the caecum.

The major typhlosole passes out of the right caecum on its anterior side, passes transversely across the anterior floor of the stomach, and enters the left caecum (LC) on its anterior side. The major typhlosole forms a broad circle within the left caecum, and terminates within the left caecum. Numerous ducts enter the left caecum from the digestive diverticula on the left side of the body. In the mouth of the left caecum, on the floor of the stomach, there is a small ridge, accompanied by a shallow groove on its posterior side. In this groove cilia beat along the groove towards the left caecum so this may be interpreted as the origin of the intestinal groove (OIG). On the anterior side of the ridge there is a small area of very faint oblique striations which lead forwards and to the right towards the transverse part of the major typhlosole. Material travelling to the left along the groove tends to pass over the ridge, on to this sorting area and up to the crest of the major typhlosole where there is a narrow rim on which cilia beat from left to right.

The dorsal hood (DH), which has a wide mouth, opens into the stomach on the left side of the mid-dorsal line. The dorsal hood is a capacious flat pocket which extends forwards over the left side of the stomach and also extends a considerable distance to the left. On the roof of the stomach anteriorly there is a series of irregular grooves (SA^8) in which cilia beat backwards, carrying particulate material from the oesophagus towards and into the dorsal hood. A well-defined sorting area on the anterior wall of the dorsal hood spreads over the roof of the stomach and down its right side (SA^3). On this sorting area cilia beat over the crests of the folds up the right side of the stomach, over its roof and towards the apex of the dorsal hood. The anterior part of this sorting area on the right side of the stomach consists of irregular lobes (L). In the grooves of this sorting area the cilia beat forwards along the grooves, between these irregular lobes, and into a rejection tract (RT) which discharges waste material into the intestinal groove (IG). The termination of this rejection tract is in an unusually anterior position, directly above the mouth of the right caecum, but material from the rejection tract passes backwards above the right caecum, which it does not enter. The sorting area is bounded anteriorly by a ridge with faint transverse striations (R). Mucus-bound

material may pass from the sorting area (SA^3) behind, over the rejection tract (RT) and on to this ridge, whence it is conveyed forwards and upwards to the dorsal hood.

A sorting area of very fine ridges and grooves lies on the left anterior wall of the stomach (SA^6) and curves backwards to enter the dorsal hood low down on its anterior wall. This sorting area may be regarded as an extension of that in the left pouch ; it collects a certain amount of material from the anterior part of the stomach, and also from the sorting area (SA^3) in the mouth of the dorsal hood, and carries it deep into the dorsal hood.

On the roof and posterior wall of the dorsal hood there is a system of ridges and grooves (SA^5) which passes from the dorsal hood, over the roof of the stomach and down its right side. Cilia on the crests of these ridges beat transversely forwards over the ridges and into a groove which bounds the sorting area anteriorly, and in which a ciliary current carries particles deep into the dorsal hood. In the grooves of this sorting area cilia beat out of the dorsal hood and down the right side of the stomach towards the orifice of the mid-gut.

The left pouch (LP) is a capacious pocket which lies between the dorsal hood and the left caecum. It passes backwards under the dorsal hood, and receives at least fifteen ducts of various sizes from the digestive diverticula on the left side of the body. The walls of the left pouch are deeply folded, and these folds are covered by a finely ridged sorting area (SA^6) which extends out of the left pouch on to the floor of the stomach and also over a globular swelling on the upper border of the left pouch, on to the left anterior wall of the stomach. Cilia on this sorting area beat backwards along the grooves, and bring particles towards the anterior border of the gastric shield.

The gastric shield (GS) is relatively small. It sends a deep saddle-shaped flare into the mouth of the dorsal hood, another flare invests the posterior and dorsal border of the left pouch, and a further lobe of the gastric shield passes forwards above the left pouch and in front of the dorsal hood. In one specimen an additional and wholly separate piece of gastric shield (GS′) was found on the posterior border of the dorsal hood.

A series of broad folds passes down the posterior wall of the stomach and enters the hemispheric pocket behind the mouth of the mid-gut, and a sorting area of finer folds (SA^{10}) lies immediately in front of this and runs down to the mouth of the mid-gut.

The portion of the intestinal groove which passes transversely across the anterior floor of the stomach is bordered anteriorly by the overhanging posterior margin of a sorting area (SA^7) of irregular folds which pass obliquely upwards to the left. There is a tendency for particles passing forwards over the floor of the stomach to be thrown forwards from the major typhlosole over the intestinal groove and on to this sorting area, on which they are conveyed towards and into the dorsal hood.

Aloididae

Aloidis (*Corbula*) *gibba* (Olivi) (Fig. 17)

Yonge (1946) briefly described and figured the interior of the stomach of *A. gibba*. His Fig. 14 is described as having been opened from the right

side, but clearly the interior of the stomach is viewed from the *left* side after having been opened by an incision on its left side. This accounts for Yonge's statement that the gastric shield covers the roof of the stomach, whereas it is here shown that it lies on the left side of the stomach. The " food-sorting caecum " described by Yonge (his Fig. 14, SC) is clearly the dorsal hood. Yonge did not discern the three separate openings of the left pouch, left caecum and right caecum, but regarded the whole anterior floor of the stomach as a single large opening from the digestive diverticula into the stomach.

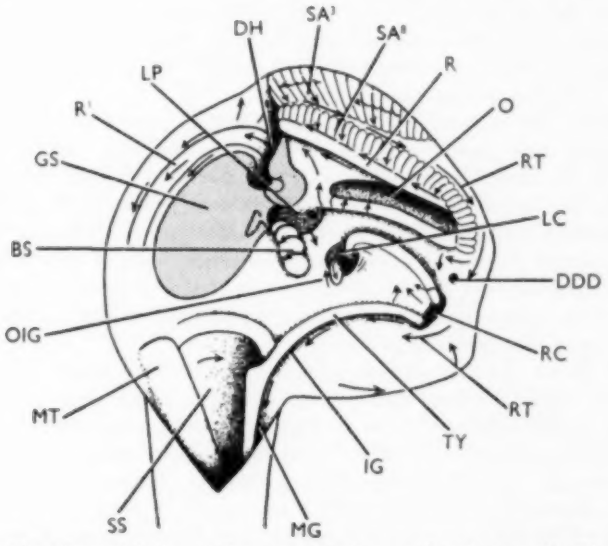

Fig. 17.—*Aloidis gibba*. Interior of the stomach after opening by a vertical incision in the posterior wall from the dorsal hood to the mid-gut. (For lettering see p. 487.)

The stomach of *Aloidis gibba* is almost globular, being slightly elongated in the vertical plane. The oesophagus, which is flattened dorso-ventrally, opens on the anterior face of the stomach by a large oval orifice (O). The combined style-sac (SS) and mid-gut (MG) passes directly downwards from the postero-ventral wall of the stomach. The minor typhlosole (MT) terminates at the mouth of the mid-gut, while the major typhlosole (TY), accompanied on its right side throughout its course by the intestinal groove (IG), passes forwards over the floor of the stomach. The major typhlosole sends a tongue into the shallow, semi-circular right caecum (RC), into which open five ducts from the digestive diverticula. A single duct (DDD) opens into the stomach independently, a little anterior to the mouth of the right caecum. Cilia in the mouths of the ducts beat outwards, towards the stomach, and the cilia on the upper surface of the tongue of the major typhlosole similarly beat outwards from the right caecum towards the stomach.

The major typhlosole crosses the anterior side of the stomach from right to left, and enters the left caecum (LC) on its anterior wall. It circles within

the left caecum and, emerging on its posterior border, terminates on the floor of the stomach just outside. The origin of the intestinal groove (OIG) is therefore on the floor of the stomach, outside the mouth of the left caecum. The number of ducts entering the left caecum from the digestive diverticula was not noted.

The dorsal hood (DH) arises on the roof of the stomach and passes over to the left side. On its anterior wall it bears a ridge (R) ventrally, and above this, two sorting areas. The ridge and the most anterior sorting area (SA^8) arise at the right corner of the orifice of the oesophagus, projecting very slightly into the oesophagus. Cilia beat transversely in the grooves crossing the sorting area, and then along the ridge into the dorsal hood. Thus potential food material arriving at the right corner of the oesophageal orifice is transported directly to the dorsal hood.

The second sorting area (SA^3) on the anterior face of the dorsal hood is slightly larger, and passes over the roof of the stomach. Cilia beat transversely over the crests of its folds, carrying particles deeper into the dorsal hood. Cilia in the grooves between the folds beat forwards along the grooves and pass material into a rejection tract (RT) which lies between the two sorting areas, and which passes down the right anterior wall of the stomach and discharges material into the intestinal groove (IG). On the posterior wall of the dorsal hood cilia beat outwards, along a ridge (R^1) which accompanies the dorsal border of the gastric shield.

The left pouch (LP) lies between the mouths of the dorsal hood and of the left caecum. About three ducts enter the left pouch from the digestive diverticula on the left side of the body, one opening anteriorly, one postero-dorsally and one postero-ventrally. There is a beaded ridge (BS) on the floor of the left pouch, on which cilia beat over the ridge, towards the gastric shield. This ridge projects on to the floor of the stomach. Anterior to the ridge, cilia on the floor of the left pouch beat outwards, from the left pouch to the stomach.

The gastric shield (GS) is moderately well developed, and invests the mouth of the dorsal hood with a firm saddle-shaped flare. The gastric shield also sends a short stiff flare over the posterior border of the left pouch.

On the left corner of the oesophageal orifice it is curious to find that cilia beat upwards from the stomach and back into the oesophagus. Particles carried back into the oesophagus in this way are then carried upwards again and out of the oesophagus on to the anterior roof of the stomach.

ADESMACEA

Pholadidae

Barnea parva (Pennant)
Barnea candida (L.)
Pholas dactylus (L.)
Pholadidea loscombiana (Turton)
Zirphaea crispata (L.)
Martesia striata L.

The stomachs of *Pholadidea loscombiana* and of *Barnea parva* were described by Graham (1949), who illustrated the interior of the stomach of the former.

The stomachs of these two species were redescribed in greater detail, and figured, by Purchon (1955), who made certain changes in the terminology adopted by Graham (1949) as indicated above for *Venus fasciata* and *Paphia pullastra* (Veneridae). An appendix to the stomach was figured and described for all members of the Pholadidae with the exception of *Zirphaea crispata* and *Martesia striata*. Purchon (1955, 1956) considered that this organ was the pre-adaptive homologue of the wood-storing organ of the Teredinidae (Potts, 1923) and of *Xylophaga dorsalis* (Purchon, 1941). The appendix was also considered to be homologous with the " postero-dorsal caecum " of the Tellinacea (Yonge, 1949). Purchon also illustrated and described the stomachs of *Barnea candida*, *Pholas dactylus* and *Zirphaea crispata* (1955), and described the stomach of *Martesia striata* (1956). No further details can as yet be added to these accounts.

Teredinidae

Psiloteredo amboinensis Taki & Habe (?) (Figs. 18 & 19)

Specimens were obtained from a fallen tree trunk which lay at the seaward margin of the mangrove reserve at Tanjong Penuru on the south-west coast of Singapore island.

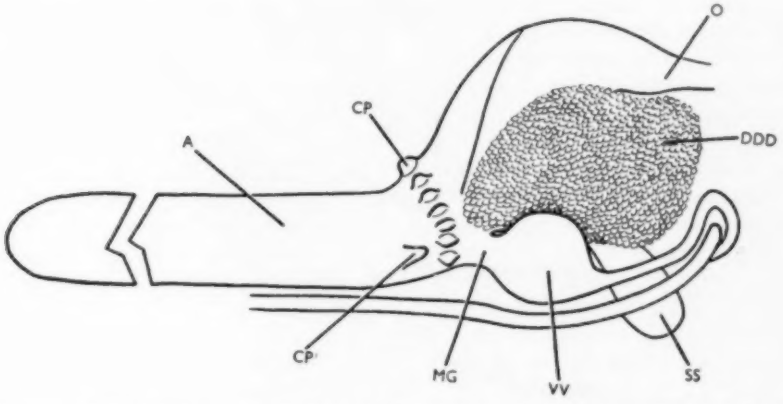

Fig. 18.—*Psiloteredo amboinensis*. (?) View of the anterior part of the alimentary canal as seen after dissection from the right side. (For lettering see p. 487.)

Fig. 18 indicates the disposition of the stomach and the associated organs after dissection from the right side. The oesophagus (O) enters the globular stomach antero-dorsally ; the digestive diverticula (DDD) form a compact mass which covers the right and anterior sides of the stomach ; the wood-storing caecum (A) arises from the postero-ventral border of the stomach and extends backwards horizontally through the visceral mass, only about one-third of its length being shown in the figure ; the right side of the orifice of the caecum is ornamented by a series of hollow conical protuberances (CP) of which seven can be seen externally in the figure ; a single, larger conical

pocket (CP') projects forwards from the ventral wall of the caecum ; the mid-gut (MG) opens into the stomach immediately in front of the orifice of the wood-storing caecum, and expands almost immediately to form a spherical valve (VV) within which the major typhlosole is very greatly dilated ; the style-sac (SS) is relatively short and is completely separate from the mid-gut.

It has been explained previously that the wood-sorting caecum of the Teredinidae is homologous with the postero-dorsal caecum of the Tellinacea (Yonge, 1949) and with the appendix of the Pholadidae (Purchon, 1955). It will be referred to henceforth in this account as the appendix.

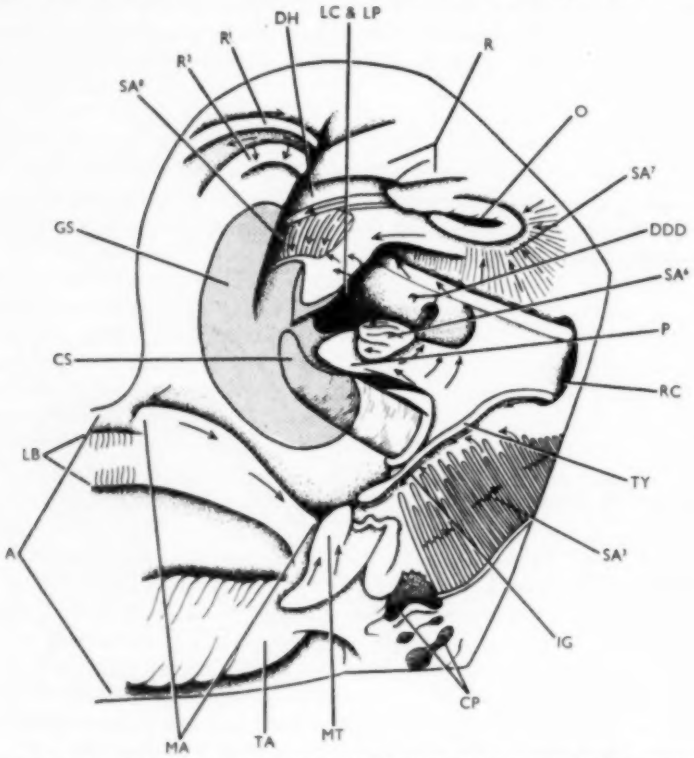

Fig. 19.—*Psiloteredo amboinensis*. (♀) View of the interior of the stomach after opening by an oblique incision in the right side passing from the appendix towards the oesophagus. (For lettering see p. 487.)

The stomach was opened by an oblique incision in its right side, passing upwards from the mouth of the appendix towards the oesophagus, and the internal structures so revealed are illustrated in Fig. 19. The orifice of the oesophagus (O) is flattened dorso-ventrally, and is overhung by a broad and fleshy fold (R) which enters the dorsal hood on its anterior face. The opening of the mid-gut is hidden from view in Fig. 19. The major typhlosole forms a massive cylindrical plug in the spherical dilatation of the mid-gut, and this

probably serves as a valve which prevents the passage of undigested particles of wood from the appendix into the mid-gut. Presumably when the stomach and appendix are well filled there will be considerable tension in the stomach wall. This tension would force some of the stomach contents into the mid-gut, but for the cylindrical dilation of the major typhlosole which is probably forced like a stopper into the succeeding narrow part of the mid-gut.

The major typhlosole (TY) emerges from the mid-gut as a thin and delicate blade which curves forwards over the right side of the stomach, accompanied throughout by the intestinal groove (IG). The major typhlosole enters the right caecum (RC), within which it is divided deeply into two lobes. About fifteen ducts enter the right caecum from the digestive diverticula, and flares of the major typhlosole push deeply into all of these ducts. The major typhlosole emerges from the right caecum and crosses the anterior floor of the stomach from right to left.

On the left side of the stomach the major typhlosole enters the left caecum (LC) which lies under the anterior border of the dorsal hood. It circles this cavity in an anti-clockwise direction as seen from the right side, and sends flares into the mouths of about fifteen ducts from the digestive diverticula ; the major typhlosole then enters and circumnavigates first an anterior chamber and then another chamber lying posteriorly near the median line, and terminates near the mouth of this last chamber. These three chambers, all of which receive ducts from the digestive diverticula (DDD), should be regarded as together forming the combined left pouch and left caecum (LC & LP).

The minor typhlosole (MT) passes out of the mouth of the mid-gut and curves backwards towards the mouth of the appendix, outside which it terminates.

The dorsal hood is very well developed ; its anterior wall bears a small sorting area (SA^{8}?), and the broad fleshy fold (R) which was mentioned above. The posterior wall of the dorsal hood bears two ridges (R^{1}, R^{2}) between which there is a ciliated rejection tract. The gastric shield (GS) is of medium size, but is very well defined, and sends a deep saddle-shaped flare into the mouth of the dorsal hood. A saddle-shaped lobe of the gastric shield passes forwards and invests the posterior floor of the chamber (LC) into which the major typhlosole passes. This suggests that in this case the left pouch has not yet become differentiated from the left caecum.

The crystalline style (CS) is short, firm, and pear-shaped. The part of the crystalline style which projects into the stomach is more slender than the part which still lies in the style sac, and the distal end of the style is soft, and tapered. Anterior to the orifice of the style-sac a tall shield-shaped prominence (P) arises from the floor of the stomach in the median line, and protects the anterior side of the crystalline style. The anterior side of this prominence bears an ill-defined sorting area (SA^{8}) which passes to the left on to the floor of the left pouch.

The appendix (A) did not contain any wood fragments, although the specimen had only very recently been removed from its burrow. A large, fleshy typhlosole (TA) hangs in the cavity of the appendix, and extends from its mouth to its distal extremity. The roof of the appendix bears a longitudinal

band (LB) which is transversely striated. These striations do not appear to function as a sorting area. It was difficult to demonstrate any ciliary currents within the appendix, these being largely confined to the mid-dorsal band (LB) on which cilia beat from the centre towards its lateral margins. In all probability the discharge of particles from the appendix into the stomach is effected by muscular contractions in the walls of the appendix. The walls of the appendix secreted mucus copiously.

There is a well-developed sorting area (SA^3) on the right side of the stomach and stretching upwards to the mouth of the dorsal hood. There is also a very delicate, and ill-defined series of striations on the anterior wall of the stomach, radiating outwards from the oesophageal orifice towards the intestinal groove (SA^7).

The purpose served by the series of hollow protuberances (CP) on the right side of the mouth of the appendix is not known.

The shell valves of the specimen dissected were examined by Miss Ruth D. Turner (the pallets were not available), who reported as follows: " Lacking the pallets it is impossible to determine the species but, on the basis of the shell and the origin of the apophysis from the middle of the shelf rather than from beneath the umbo, it is probably *Psiloteredo amboinensis* Taki and Habe (1945). Bartsch (1927) created a new genus and species *Eoteredo philippinensis* which he based on dead, broken specimens of shells only and this may be the same species as that described by Taki and Habe. However, since Bartsch did not have the pallets it is impossible to place his species, and both the genus and the species must remain *nomena nuda*. Consequently though Bartsch's work has several years priority the later name of Taki and Habe which is based on recognisable material is being used ".

Teredo manni Wright

Specimens of this species were obtained from the same log as was the specimen of *Psiloteredo* described above. At first inspection the interior of the stomach was very similar to that of the previous species but the following important differences were noted :—

1. The right caecum was small, semi-circular in shape and received only six ducts from the digestive diverticula. The major typhlosole did not subdivide into two lobes within the right caecum, nor did it send flares into the mouths of the ducts.
2. The major typhlosole did not enter the wide pocket on the left side of the stomach which lay anterior to the mouth of the dorsal hood, and which received many large ducts from the digestive diverticula. This cavity is clearly the left pouch, which was not isolated from the left caecum in the previous species described.
3. The major typhlosole entered a long slender left caecum which extended backwards to the extremity of the visceral mass and which received ducts from the digestive diverticula at intervals along its course. The major typhlosole penetrated this left caecum to its apex, then returned and terminated on the floor of the stomach anterior to the base of a large

shield-shaped prominence comparable with that described for *Psiloteredo* described above.

4. The mouth of the appendix was not ornamented with hollow conical protuberances.
5. The mouth of the mid-gut was wide, and the spherical expansion of the mid-gut was further forward, at a greater distance from the opening of the mid-gut into the stomach.
6. A flap accompanied the major typhlosole and covered the intestinal groove in the left caecum and in the stomach.

Teredo navalis L.

Lazier (1924) reviewed previous literature on the anatomy of the alimentary canal in the Teredinidae, and gave an excellent illustrated account of the internal structure of the alimentary canal of *T. navalis*. It is only necessary here to interpret his figures and description in the light of present knowledge and terminology, and to point out a few anatomical differences between the alimentary canals of *T. navalis* and of the two species described here.

Whereas the stomachs of the two species described in this paper are globular, the stomach of *T. navalis* is greatly elongated. Lazier states that "the gastro-intestinal typhlosole (= major typhlosole) originates at the hepatic orifice in the lateral pouch (= left pouch), passes across the stomach below the opening of the oesophagus and posteriorly along the right ventral wall to the posterior hepatic orifice (= orifice of the right caecum) which it enters. After circling the lumen of the posterior liver (= right caecum) it emerges at the dorsal edge of the orifice and passes posteriorly and ventrally into the intestine (= mid-gut)". The only possible interpretation of this configuration is that the elongated "posterior liver" is the right caecum, which has been lengthened and displaced posteriorly. Lazier stated that this was the part of the digestive diverticula which consisted of two histologically distinct portions.

The caecum (= appendix) of *T. navalis* contains an "elaborate two-coiled typhlosole" Lazier concluded that this was the site of digestion of the fragments of wood which remain for a considerable time in the caecum, and he commented that the typhlosole offered a large area for absorbtion and was adequately supplied with blood.

Lazier mentions, but does not describe in detail, the dorsal caecum (= dorsal hood), and the lateral pouch (= left pouch).

DISCUSSION

The major part of the present paper is devoted to the description of examples of Stomach Type V which is now known to occur in twenty-one families of Eulamellibranchia. Details of variation in structure in these twenty-one families are set out in Table 1, and are discussed individually below.

1. *The relation between the style-sac and the mid-gut.* The style-sac and mid-gut are conjoined in the majority of cases, the exceptions being the Dreissenidae, Mactridae, Mesodesmatidae, Solenidae, Myidae, Pholadidae and Teredinidae. As was stated by Yonge (1949), this difference has no systematic significance.

2. *The course taken by the major typhlosole and the intestinal groove.* Typically these structures pass forwards from the mouth of the mid-gut and enter the right caecum and emerge again on the anterior side having penetrated the caecum in the form of a semi-circular or elongated tongue. The major typhlosole and intestinal groove then cross the anterior floor of the stomach from right to left, enter the left caecum, and form a similar tongue within the left caecum. This is true of the great majority of examples studied, the only additional or exceptional features being as follows :— In the Psammobiidae (Figs. 13 & 14) in addition a stiff semi-circular elevation sweeps across the floor of the stomach from the mouth of the mid-gut to that of the left pouch in much the same way as does the major typhlosole in stomachs of Type IV (Purchon, 1957, 1958). This structure is not accompanied by a branch of the intestinal groove, does not function as a typhlosole, and may perhaps be dismissed as an " ornamental " feature. In the Myidae there was not the usual continuity between the major typhlosole of the mid-gut and that of the stomach. In the Chamidae the major typhlosole forms two tongues on the right side of the stomach. The smaller of these enters a small " accessory right caecum " while the larger enters the right caecum. On the left side of the stomach the major typhlosole is unusual in that it divides to form three tongues within the left caecum. The intestinal groove accompanies the major typhlosole and passes round all of these tongues. The structure of the stomach in *Chama lazarus*, described above, differs very considerably from that of *C. multisquamosa* previously described (Purchon, 1958), in which the stomach is of Type IV. The occurrence of stomachs of types IV and V within the same genus will be considered below.

3. *The form of the gastric shield.* The gastric shield lies on the left side of the stomach and invests the mouths of the dorsal hood and the left pouch with saddle-shaped flares. This was true in all cases and the only peculiarity noted was the Mactridae where the postero-ventral part of the gastric shield was extensively emarginated.

4. *The occurrence of an appendix.* This organ has been found in all families of the Tellinacea, i.e. the Donacidae, Tellinidae, Psammobiidae and Semelidae, where it was first discovered and described under the name " postero-dorsal caecum " by Yonge (1949). It also occurs in all families of the Adesmacea, i.e. the Pholadidae, Xylophaginidae and Teredinidae. Purchon (1941, 1955) showed that the appendix of the Pholadidae was in every way comparable with the food-storing caecum of *Xylophaga* and of *Teredo*, and concluded from the structural and functional similarity between the postero-dorsal caecum of the Tellinacea and the appendix of the Adesmacea that these structures are homologous and provide reliable evidence of relationship between these two groups. It was suggested that the organ should be termed the " appendix " to avoid confusion with the other stomach caeca. The present survey has failed to demonstrate any other examples of the occurrence of the appendix.

5. *The entry of ducts from the digestive diverticula.* The ducts from the digestive diverticula open into the stomach via the left pouch, the left caecum

and the right caecum. In a small majority of families in addition one or more ducts open into the stomach independently on its right side. The presence or absence of such independent ducts on the right side of the stomach cannot be regarded as of systematic significance, due to variation which has been observed within individual families. Thus in the Veneridae there are three such ducts in *Gafrarium minimum* (Fig. 8), one in *Venus fasciata* and none in *Paphia pullastra* (Graham, 1949). In the Ungulinidae there is similar variation within the genus *Diplodonta*, there being a group of seven independent ducts in *D. rotundata*, four ducts in *D. punctata*, and only one in *D. aspera* (Allen, 1958). It is therefore probable that by further study examples of such independent ducts would be found in at least some of the families in which such records are at present lacking.

6. *The distribution of the sorting areas of the stomach.* It was previously suggested (Purchon, 1958) that two sorting areas might come into contact and so harmonize with each other that it would be impossible for the investigator to recognize the occurrence of both. A sorting area may diminish in extent and definition and may perhaps be overlooked, while a ciliated area may acquire corrugations and so simulate a sorting area. For these reasons it is not easy to make an objective analysis of the occurrence and identities of the various sorting areas. The presence or absence, and the degree of development of the various sorting areas has a profound effect on the appearance of the interior of the stomach, and may obscure more fundamental issues such as the course taken by the major typhlosole and the intestinal groove. Two examples were studied in the Psammobiidae ; in *Asaphis deflorata* (Fig. 14) six different sorting areas were recognized, while in *Gari togata* (Fig. 13) only two sorting areas were seen. These were the sorting area of the left pouch (SA^6) and the sorting area on the anterior roof of the stomach (SA^8). While seven different sorting areas are listed for the Psammobiidae (see Table 1), only one of these (SA^6) is possessed by both genera. Clearly, therefore, the occurrence of sorting areas can only be used with the greatest caution for phylogenetic purposes.

The majority of the sorting areas mentioned below have already been described (Purchon, 1958) and only new sorting areas will be described here.

(*a*) *The anterior sorting area* (SA). This is only present in the Corbiculidae, *Asaphis* in the Psammobiidae in both of which it is restricted to the vicinity and interior of the left caecum, and in the Pholadidae in which it was recorded only in *Zirphaea crispata* (Purchon, 1955).

(*b*) *The principal sorting area of the dorsal hood* (SA^3). This is present in all families studied except for the Tellinidae. Graham (1949) stated that the posterior sorting area was less noticeable in *Tellina crassa* than in any other examples studied by him, but the area indicated in his figure does not seem to correspond with the sorting area now under consideration. The account of the stomach of *Tellina tenuis* by Yonge (1949) suggests that this sorting area is present, but the question is not settled beyond all doubt. It is very probable that this sorting area will be demonstrated in due course in some

TABLE I.

Analysis of variations in the structure of the stomach

		Clavagellidae	Donacidae
1	The style-sac and mid-gut are conjoined	+	
	The style-sac and mid-gut are separate		+
2	The major typhlosole penetrates both left and right caecea		
	The major typhlosole branches on left and right sides of the stomach		
	An additional semi-circular elevation crosses the floor of the stomach		
	There is a break in the major typhlosole at the mouth of the mid-gut		
	The major typhlosole does not enter a right caecum	+	+
3	The gastric shield is normal, and invests the mouths of the dorsal hood and the left pouch	+	+
	The gastric shield has retreated somewhat from the left wall of the stomach		
4	An appendix (= postero-dorsal caecum) is present		+
5	Ducts from the digestive diverticula open into the stomach via the left pouch, left and right caeca		
	In addition some ducts open independently on the right side of the stomach		
	There is no right caecum	+	+
6	SA On the anterior floor of the stomach	+	+
	SA^3 On the roof or anterior side of the dorsal hood and sometimes extending over the right wall of the stomach	+	+
	SA^5 On the posterior wall of the dorsal hood		
	SA^6 In the left pouch		+
	SA^7 Immediately below the oesophageal orifice		
	SA^8 On the anterior roof of the stomach, leading back from the oesophageal orifice into the dorsal hood	+	
	SA^{10} Adjacent to the orifice of the mid-gut		
	SA^{11} At the mouth of the appendix		
7	A fold passes transversely across the anterior floor of the stomach between the oesophagus and the intestinal groove		+
	There is a series of large pinnate lobes on the ventral and right borders of the oesophageal orifice		

(+) signifies less clearly defined.

Corbiculidae	Charnidae	Dreissenidae	Ungulinidae	Isocardiidae	Cyprinidae	Libitinidae	Cardiidae	Tridacnidae	Veneridae	Glauconomyidae	Petricolidae	Mactridae	Mesodesmatidae	Tellinidae	Psammobiidae	Solenidae	Myidae	Aloididae	Pholadidae	Teredinidae
+	+		+	+	+	+	+	+	+	+	+			+	+			+		
		+										+	+			+	+		+	+
+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
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? signifies identity is uncertain.

member of the Tellinidae and it may be stated confidently that the occurrence of this sorting area is typical of Stomach Type V.

(*c*) *The sorting area on the posterior wall of the dorsal hood* (SA^5). As in the case of Stomach Type IV, this is only of sporadic occurrence, being found in the Corbiculidae, Isocardiidae, Libitinidae, Mactridae, Mesodesmatidae, Tellinidae, Solenidae and Myidae, in all of which it is moderately well developed.

(*d*) *The sorting area of the left pouch* (SA^6). This is present in the majority of families studied, being least well developed in the Cyprinidae and Chamidae. It is probable that further studies will reveal its presence in some of the families in which it has not yet been recorded.

(*e*) *The sorting area below the orifice of the oesophagus* (SA^7). As in the case of Stomach Type IV (Purchon, 1958), distribution of this sorting area is somewhat sporadic. In the Psammobiidae it is present in *Asaphis* (Fig. 14) but is absent in *Gari* (Fig. 13). It is present in *Chama multisquamosa* (Purchon, 1958), but is absent in *C. lazarus* (Fig. 4).

(*f*) *The sorting area on the anterior roof of the stomach* (SA^8). In many cases this forms a well-defined sorting area which passes over the roof of the stomach from the right side of the oesophagus to the anterior wall of the dorsal hood, but in other cases it is represented by a less clearly defined pattern of ridges, as in the Myidae (Fig. 16) and the Corbiculidae (Fig. 3). In the Psammobiidae there is a well-defined, but rather unusual sorting area on the anterior roof of the stomach of *Gari togata* (Fig. 13), but the sorting area is absent in the case of *Asaphis*. In the Teredinidae it is confined to the dorsal hood.

(*g*) *The sorting area adjacent to the orifice of the mid-gut* (SA^{10}). This small sorting area, which has not previously been recorded, has only been recorded in three families, the Mesodesmatidae, Myidae, and the Psammobiidae; in the last-named family it has been recorded in *Asaphis* (Fig. 14) but not in *Gari*.

(*h*) *The sorting area in the mouth of the appendix* (SA^{11}). This sorting area has been found only in *Asaphis* in the Psammobiidae (Fig. 14). It might occur in other members of the Tellinacea and Adesmacea, in which an appendix is present.

7. *Other structures.* In a number of families there is a well-defined fold on the anterior floor of the stomach, between the orifice of the oesophagus and the transverse part of the intestinal groove. This fold passes up the right side of the stomach, over the roof and into the dorsal hood on its anterior wall. This structure is particularly well developed in the Psammobiidae, and in *Zirphaea* only in the Pholadidae. The same structure is present, though less well developed, in the Donacidae and in the Dreissenidae. In the Mactridae, Mesodesmatidae and in *Pholadidea* in the Pholadidae there is a series of large pinnate lobes in lieu of the above-mentioned fold, and in view of the lobation of the fold in *Zirphaea* it may well be that the fold and the lobes are comparable manifestations. In the Mactridae these lobes encircle the oesophageal orifice, the lobes on the dorsal side being smaller and simpler. In the Mesodesmatidae the lobes diminish in size dorsally, and merge with the lower border of a sorting area, while in *Pholadidea* the transition from lobes to sorting area is more abrupt.

It is clear from this review of variation in structure of the stomach in these twenty-one families that there is no single major criterion, and no grouping of minor criteria, by which these families should be sub-divided into two or more groups of families. In fact the survey reveals a singular homogeneity of structure, in spite of the gross differences in appearance which stem mainly from variations in extent of the sorting areas. The limited occurrence of the appendix strengthens the suggestion previously made (Purchon, 1955) that the Tellinacea and the Adesmacea are very closely related.

The distinction between Stomach Types IV and V is striking, and it is the view of the writer that the form of Stomach Type V is so remarkable that it could not have arisen by chance on two or more occasions. In other words, the group of families which possess this type of stomach is homogeneous and monophyletic. Until a relatively late stage in this survey it was tempting to think that those families in which the stomach was of Type IV might similarly prove to be monophyletic, but the form of this type of stomach is considerably simpler and the possibility cannot be excluded of its emergence in two or more independent phylogenies by parallel or by convergent evolution. Evidence has gradually accumulated which precludes the possibility of the detailed recognition of two phylogenies in the Eulamellibranchia, one characterized by Stomach Type IV and the other by Stomach Type V. This evidence is set out in Table 2.

TABLE 2

Examples of the occurrence of Stomach Types IV and V in the same systematic group.

Group	Examples with Stomach Type IV	Examples with Stomach Type V
Sphaeriacea	Sphaeriidae	Corbiculidae
Lucinacea	Lucinidae	Ungulinidae
	Thyasiridae	
Tellinacea	Donacidae	Psammobiidae
		Tellinidae
Chamidae	*Chama multisquamosa*	*C. lazarus*

As mentioned above it is highly improbable that a stomach of Type V could have evolved independently in a number of distinct lineages, because the relationships which are diagnostic of Stomach Type V are so complex. The theory has been advanced elsewhere (Purchon, 1958 a ; 1959) that Stomach Type IV is a primitive feature from which there evolved on the one hand Stomach Type III which is characteristic of most of the Filibranchia*, and on the other hand Stomach Type V which characterizes approximately one-half of the families in the Eulamellibranchia. If this is true it might be possible for the stomach to revert from Type V to the ancestral Type IV independently in two, three or even more lineages, and at any taxonomic level. This reversion could be effected as part of a general simplification of parts accompanying reduction of size. This theory could be advanced to account for the occurrence of a stomach of Type IV in the Sphaeriidae,

* This does not imply that the Filibranchia arose from the Eulamellibranchia.

Thyasiridae, and in *Chama multisquamosa*, as all of these are smaller than their relatives which possess stomachs of Type V, as listed in Table 2.

If Stomach Type IV is a primitive, ancestral feature it may be recapitulated in the ontogeny of species which possess stomachs of Type V in the adult stage. A search should be made for evidence on this question. If this should prove true, reversion from Stomach Type V to Type IV would also seem to be possible at any taxonomic level through a process of " juvenilisation ". This could occur in parallel in more than one lineage, and would not necessarily be related to any diminution in size of the individual. It is concluded, therefore, that in the Sphaeriidae, Lucinidae, Thyasiridae, Donacidae, and in *Chama multisquamosa* the stomach has secondarily acquired the ancestral form. Reasons may yet be advanced for taking a similar view of other examples in which the stomach has been assigned to Type IV.

The survey of the structure of the stomach throughout the Lamellibranchia seems to indicate the existence in this Class of five main phylogenies typified in general by the respective possession of the five different types of stomach. Due to the possibility of secondary simplification of the stomach as indicated above, it will not always be possible to use the structure of the stomach as a diagnostic of the phylogeny to which a particular species, genus, family or sub-order belongs. Nevertheless it is possible to use the structure of the stomach in order to gain a broad outline of the chief phylogenies within the class, using other criteria where appropriate to determine the details of the scheme.

It is concluded from the above considerations that the distribution of stomachs of Types IV and V as shown in Table 2 is not inconsistent with the view that in general the internal structure of the stomach can be used as an indicator of the phylogenetic structure of the class Lamellibranchia.

Allen (1958) reviewed the basic form and adaptations of the Lucinacea and concluded that this group consisted of three families, the Ungulinidae, Lucinidae and Thyasiridae. Of these he considered the Ungulinidae to be most primitive, and the Thyasiridae and Lucinidae to be more highly evolved and modified. In these last two families there is simplification of the stomach including the loss of the sorting areas and reduction of the number of apertures leading from the stomach to the digestive diverticula and an increase in the size of these apertures, the purpose of this simplification being to facilitate the acceptance of large particles. As shown in the present survey this is further aided by reversion of the stomach from Type V to Type IV by withdrawal of the tongues of the major typhlosole from association with the ducts from the digestive diverticula. As stated by Allen (1958) this does indeed lead to a better understanding of the mechanisms of the stomach in the Eulamellibranchia. The extreme reduction of the sorting areas in the Thyasiridae and Lucinidae to facilitate the acceptance of large particles in these two families is very powerful support of the views of Purchon (1955) that in the Pholadidae " The greater part of the ciliary currents in the stomach appeared to be concerned with preventing particles from entering the ducts of the digestive diverticula ". The ciliary sorting areas—which may well be thought of largely as trapping areas—are well developed in the rock-boring

Pholadidae and in very many other families in which it is evidently desirable to hinder approach to the ducts to the digestive diverticula by unwanted large particles or excessive quantities of small particles. They are reduced in the Thyasiridae and Lucinidae where such hindrance is evidently not desirable. Thus the findings of Allen (1958) for the Lucinacea fit in well with the views expressed by the present writer in many papers (Purchon, 1955, etc.) notwithstanding Allen's surprising statement to the contrary.

Some preliminary consideration has already been given to the application of the results of this survey to the elaboration of a phylogenetic classification of the Lamellibranchia (Purchon, 1958 a ; 1959 ; 1960).

KEY TO THE LETTERING OF THE FIGURES

A	Appendix (*Donax*, *Gari*, *Asaphis*, *Teredo*).
AT	Acceptance tract.
ARC	Accessory right caecum (*Chama*).
B	Blind pocket on the right side of stomach (*Chama*, *Geloina*, *Gari*).
BS	Beaded swellings (*Gari*, *Aloidis*).
CP, CP′	Conical protuberances on appendix (*Teredo*).
CS	Crystalline style.
DH	Dorsal hood.
DDD	Orifices of ducts from the digestive diverticula.
DDD^{1-7}	Orifices of ducts from the digestive diverticula.
E	Semicircular elevation on floor of stomach (*Asaphis*, *Gari*).
EL	Forwardly projecting elevation on right side of stomach.
F	Folds on the anterior face of the stomach (*Donax*).
FA	Folded area on posterior floor of stomach (*Caecella*).
FD	Irregular folds.
FP	Fleshy pad in the entrance to the appendix.
G	Groove leading to the dorsal hood (*Geloina*, *Cyprina*).
GS	Gastric shield.
GS′	Additional piece of gastric shield (*Mya*).
GR	Groove joining the mouths of the style-sac and mid-gut.
H	Hemispheric pocket at the mouth of the mid-gut (*Mactra*, *Mya*, *Caecella*).
IG	Intestinal groove
L	Irregular lobes.
LB	Longitudinal band in the appendix (*Teredo*).
LC	Left caecum.
LP	Left pouch.
MA	Mouth of the appendix (*Donax*, *Gari*, *Teredo*).
MG	Mid-gut.
MT	Minor typhlosole.
O	Oesophagus.
OIG	Origin of the intestinal groove.
P	Prominence on floor of stomach (*Teredo*).
PP	Irregular papillae (*Cyprina*).
PR	Processes ornamenting the oesophageal orifice (*Mactra*, *Atactodea*, *Caecella*).
R	Ridge passing from the dorsal hood to the oesophageal orifice or past its right side on to the anterior floor of the stomach.
R^1, R^2	Ridges on the posterior wall of the dorsal hood.
R^3	Ridge on floor of stomach (*Caecella*).
RB	Beaded ridge entering the dorsal hood (*Geloina*).
RC	Right caecum.
RC^1	Right caecum, cut open (*Atactodea*, *Caecella*).

RG	Rejection groove (*Cyprina*).
RM	Rim to the oesophageal orifice.
RT	Rejection tract.
RT′	Additional rejection tract (*Gari*).
S	Oval swelling of the gastric shield (*Donax*).
SA	The anterior sorting area.
SA^3	Principal sorting area of the dorsal hood.
SA^5	The sorting area on the posterior wall of the dorsal hood.
SA^6	The sorting area of the left pouch.
SA^7	Sorting area below the oesophageal orifice.
SA^8	Sorting area on the anterior roof of the stomach.
SA^{10}	Sorting area at the mouth of the mid-gut.
SA^{11}	Sorting area in the mouth of the appendix.
SP	Spiral of major typhlosole, in mouth of left caecum.
SS	Style-sac.
STR	Striations in the mouth of the right caecum (*Chama*).
SW	Swelling in the mouth of the left pouch (*Geloina*).
T	Tooth of the gastric shield.
TA	Typhlosole in the appendix (*Teredo*).
TY	Major typhlosole.
TY^1	Transverse part of the major typhlosole.
UP	Swelling on right wall, which arches over the intestinal groove (*Mactra*).
UR	"U"-shaped ridge on right wall (*Donax*).
V	Vestibule, or anterior chamber of stomach (*Chama*).
VV	Spherical valve of mid-gut (*Teredo*).

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